University of Alberta

Multi-scale Habitat Selection by Mountain Caribou in West Central Alberta

By

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Master of Science

in

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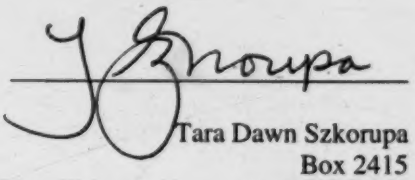

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ABSTRACT

Woodland caribou (*Rangifer tarandus caribou*) populations in Alberta are in decline, which may be partially attributed to habitat loss and alteration resulting from industrial activities. An understanding of caribou habitat requirements is a fundamental first step towards conservation of the species. In this study, I analysed winter habitat selection by mountain caribou, an ecotype of woodland caribou, in west central Alberta (1998-2001). Global Positioning System (GPS) data, from female caribou, were used to analyse caribou habitat selection for home ranges, and for general habitat use within home ranges. Snow tracking was used to quantify caribou foraging behaviour over a range of snow conditions, and to determine the habitat and snow conditions associated with foraging sites.

For their home ranges, caribou generally preferred older, denser stands. For general habitat use within their home ranges, caribou showed an even greater preference for older stands, and again preferred denser stands. I found that caribou fed on tree lichens more as snow hardness increased, although there was no corresponding decline in cratering (i.e. digging through the snow for ground forage). Cratering sites were associated with moderately dense stands (around 50% canopy closure), and shallow, soft snow. Arboreal feeding sites were associated with old stands containing greater amounts of spruce (*Picea spp.*).

My research demonstrates that mountain caribou require a suite of winter habitats, at multiple spatial scales, to accommodate a range of snow conditions. I discuss specific recommendations for long-term habitat management.

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CHAPTER 1 - INTRODUCTION

Habitat loss and alteration may be threatening the persistence of woodland caribou (*Rangifer tarandus caribou*) in Alberta (Dzus 2001). Populations of woodland caribou are declining, which led to a provincial "threatened" designation in 1985, and again when reviewed in 2001. Two ecotypes of woodland caribou are recognised in Alberta (Edmonds 1998). The mountain ecotype inhabits the mountains and foothills of west central Alberta, while the non-migratory boreal ecotype is generally found in peatland habitats throughout central and northern Alberta. Both ecotypes extend well beyond the province of Alberta, and were recently listed as nationally "threatened" by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). In west central Alberta, the Redrock/Prairie Creek winter range supports a herd of about 300 mountain caribou. However, this range has been largely allocated to forestry companies (Hervieux et al. 1996), which creates the potential for significant loss or alterations in habitat (Cumming 1992). To maintain caribou populations, we must first understand their habitat needs, and then ensure sufficient supplies of required habitat over time.

My research was undertaken as part of a larger research program in west central Alberta that covers topics such as wolf-caribou relationships, and the response of caribou to industrial development (Kuzyk 2001; Oberg 2001). Government and industrial land-users raise pertinent questions related to caribou management through the West Central Alberta Caribou Standing Committee (WCACSC), which may then be addressed through scientific study. Forestry companies and provincial wildlife

managers agree that one of the major gaps in knowledge is the specific habitat requirement of mountain caribou in Alberta (Brown 1998). This provided the incentive for my habitat selection research.

The habitat requirements of caribou in west central Alberta need to be further defined. Although there has been habitat research on these caribou (Bjorge 1984; Edmonds and Bloomfield 1984; Stepaniuk 1997), analyses were conducted at broad spatial and temporal scales. Spatially, past habitat research has been restricted to single scale analyses, and has lacked the level of detail attainable by current advancements in GIS (Geographic Information System) and GPS (Global Positioning System) technology. Temporally, past research has averaged habitat use patterns over entire seasons, which may have concealed variation at finer temporal scales (such as during critical periods, when snow conditions are harsh).

Habitat selection patterns typically occur at multiple spatial scales (e.g., Wiens 1989; Apps and Kinley 2000; Schneider et al. 2000; Apps et al. 2001). My study extends the current understanding of mountain caribou habitat selection by conducting analyses at several spatial scales. Others have proposed that caribou may select habitats for predator avoidance at broad spatial scales, and then select habitats for forage at finer scales, within habitats that are relatively free of predation risk (Bergerud et al. 1990; Rettie and Messier 2000). Therefore, caribou habitat requirements at multiple scales must be understood and managed for, to ensure that both forage and anti-predator needs are met. When planning for caribou habitat, managers must also recognise that caribou require sufficient preferred habitat to space out across the landscape (Cumming 1992; Hervieux et al. 1996). Although caribou

travel in small groups throughout the winter, maintaining low densities across their range is thought to be a fundamental anti-predator tactic (Bergerud and Page 1987).

Selection patterns also occur at multiple temporal scales, both within and among years. To determine which habitats should be maintained, we need to know not only what caribou typically use, but also their requirements during critical periods, such as harsh winters, which may limit survival and reproduction. A major source of ecological variability in winter stems from fluctuating snow conditions. Harsh snow conditions can have negative impacts on caribou populations, especially if sufficient required habitat is not available (Hyvarinen et al. 1977; Reimers 1977; Simpson et al. 1985; Adamczewski et al. 1986; Gates et al. 1986). Such potential bottlenecks occur during extreme winters, and during the late winter of most years, when snow is typically deeper and harder than in early winter. Caribou employ two main foraging strategies in the winter: they either crater (dig through the snow) for terrestrial lichens and forbs, or forage on arboreal lichens (which grow on trees). Although caribou are well adapted to cratering (Telfer and Kelsall 1984), very deep or hard snow may force caribou to switch to feeding on arboreal lichens (Bergerud and Nolan 1970; Simpson et al. 1985; Rominger and Oldemeyer 1989). The importance of arboreal lichen as forage for west central Alberta caribou has not been quantified, and information is lacking about the habitats selected for arboreal feeding (Brown and Hobson 1998).

For long-term habitat supply planning, land-use and wildlife managers require detailed information on caribou habitat needs at multiple spatial scales and at fine temporal scales (e.g., as snow conditions change over the winter and between years).

For example, at present, forests with adequate supplies of terrestrial lichens for foraging are targeted in habitat supply planning. However, failure to maintain a supply of stands high in arboreal lichens may lead to a reduction in caribou populations. Thus, information on the suite of habitats required by caribou is essential for ensuring that habitat-altering practices such as timber harvesting do not compromise caribou conservation.

THESIS OVERVIEW

The overall objective of my study was to provide quantitative information on the habitat requirements of mountain caribou in Alberta. I used multi-scale analyses, and studied habitat selection over a range of snow conditions, because I predicted that caribou would require a suite of habitat characteristics, over space and time, to meet their needs.

In Chapter 2, I analyse habitat selection for home ranges within the larger study area, and for general habitat use within home ranges, using GPS data from collared caribou and GIS computer mapping. In Chapter 3, data collected through snow tracking is analysed, which complements the broad scale analyses in Chapter 2 by providing more detailed information about caribou foraging in different habitats. Field data on arboreal and terrestrial lichen foraging, and snow conditions, helps to clarify the importance of different habitats to caribou. Finally, in Chapter 4, I provide a review and synthesis of my findings, expand on the management implications for land-use in west central Alberta, and discuss opportunities for future research.

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CHAPTER 2 - HABITAT SELECTION FOR HOME RANGE AND GENERAL HABITAT USE BY MOUNTAIN CARIBOU IN ALBERTA

INTRODUCTION

Each year, the Redrock/Prairie Creek mountain caribou (an ecotype of woodland caribou, *Rangifer tarandus caribou*; Edmonds 1998) migrate into the upper foothills of the Rocky Mountains for the winter. The winter range provides a mosaic of forest stands required by caribou for foraging, avoiding predators and fulfilling other life requirements. Although this herd's mountainous summer range is largely protected, forestry and other human activities are increasing across the winter range. This has raised concerns about the quality and quantity of habitat available to these caribou (Edmonds 1988; Hervieux et al. 1996; Brown and Hobson 1998), and about the impacts of industrial development on caribou during a time of year that can be particularly critical (Hyvarinen et al. 1977; Simpson et al. 1985; Gates et al. 1986; Adamczewski et al. 1988; Nellemann 1996). Since caribou populations are declining across Alberta (Edmonds 1998; Dzus 2001; but see Bradshaw and Hebert 1996), sound habitat supply planning and management is critical.

Caribou across North America use different habitats, depending on the availability of habitats and forage, interactions with predators, and environmental conditions such as snow depth. For example, woodland caribou are adapted to diverse, local habitats, such as very old engelmann spruce (*Picea engelmannii*) - subalpine fir (*Abies lasiocarpa*) stands in deep snow areas of British Columbia (Rominger and Oldemeyer 1989), and large peatland complexes in northern Alberta

(Bradshaw et al. 1995). The variable nature of caribou habitat selection necessitates area-specific research. In the foothills of west central Alberta, research spanning two decades has yielded important information on population trends, range extent, response of caribou to industrial activity and broad habitat use patterns (Bjorge 1984; Edmonds and Bloomfield 1984; Thomas et al. 1996; Stepaniuk 1997; Smith et al. 2000; Oberg 2001). However, detailed information required for habitat supply planning is still lacking, and has recently been identified as a knowledge gap by both government and industry (Brown 1998; Brown and Hobson 1998).

The specific objective of my study was to determine which forest stand characteristics are important for wintering caribou. I conducted analyses at two spatial scales because selection patterns may differ among scales (e.g., Wiens 1989; Apps and Kinley 2000; Schneider et al. 2000; Apps et al. 2001). Multi-scale analyses also lead to a greater understanding about the scales at which animals relate to their environment (Morris 1987). I chose to examine selection at coarse and fine spatial scales, corresponding to Johnson's (1980) 2nd order (home range selection within a larger study area) and 3rd order (habitat selection within an animal's home range).

Others have proposed that caribou select habitats at coarser scales to avoid predators, and then select foraging areas at a finer scale, within areas that are relatively safe from predators (Bergerud et al. 1990; Rettie and Messier 2000). Caribou are thought to avoid predators, in part, by separating themselves spatially from alternate prey (Cumming 1992; Seip 1992). Caribou tend to inhabit areas that have low numbers of moose (*Alces alces*), deer (*Odocoileus spp.*) and elk (*Cervus elaphus*), because these alternate prey attract wolves. Since these species generally

prefer younger forests, and areas with abundant browse (Telfer 1978; Schwartz and Franzmann 1989), I predicted that caribou would avoid these habitats at a coarse scale, to reduce their chance of encountering wolves.

At a fine scale, I predicted that caribou would select forest stands that have abundant forage. In west central Alberta, caribou mostly "crater" (dig through the snow) for terrestrial (ground) lichens throughout the winter (Edmonds and Bloomfield 1984; Stepaniuk 1997). However, arboreal (tree) lichens may be important in this area when snow is deep and/or hard (Edmonds and Bloomfield 1984; Hervieux et al. 1996; Brown and Hobson 1998; Chapter 3). Terrestrial lichens are most abundant in semi-open lodgepole pine (*Pinus contorta*) stands that are over 75 years old, while arboreal lichens are most abundant in spruce (*Picea spp.*) forests over 130 years old (Ahti and Hepburn 1967; Edmonds and Bloomfield 1984; Thomas et al. 1996; Rettie et al. 1997; Chapter 3). Therefore, I predicted that caribou would select semi-open pine stands over 75 years old, for terrestrial feeding and general habitat use over the winter. I further predicted that, in late winter, when snow is generally deeper and harder than in early winter (Edmonds and Bloomfield 1984), caribou would select older (130+ years old), spruce stands, for arboreal feeding. Although I propose specific habitat selection predictions for predator avoidance (coarse scale) and forage abundance (fine scale), these two explanations are not mutually exclusive, because many of the habitats selected by caribou may meet both their anti-predator and forage needs.

METHODS

Study Area

This study was conducted within the Redrock/Prairie Creek caribou winter range in west central Alberta (54°N, 119°W) (Figure 2-1). The study area (about 2000 km^2) extends north and south of the Kakwa River, along the eastern slopes of the Rocky Mountains. This upper foothills landscape is intersected by ridges and many small drainages. Industrial use includes timber harvesting, oil & gas exploration and development, and coal mining. The area is also used for both motorised and non-motorised recreation.

In addition to the estimated 300 mountain caribou (Brown and Hobson 1998), there are moose throughout the area, and smaller, more localised, populations of elk, mule deer (*Odocoileus hemionus*) and white-tailed deer (*Odocoileus virginianus*). Bighorn sheep (*Ovis canadensis*) and mountain goat (*Oreamnos americanus*) are present in alpine areas, in the extreme southern part of the study area. Other large mammals include coyotes (*Canis latrans*), wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), black bears (*Ursus americanus*) and cougars (*Felis concolor*). Main conifer species are black spruce (*Picea mariana*), engelmann spruce, white spruce (*Picea glauca*), subalpine fir, and lodgepole pine. The most abundant arboreal lichens are *Bryoria spp.* and *Usnea spp.*, while common terrestrial lichens are *Cladina spp.*, *Cladonia spp.*, *Cetraria spp.* and *Peltigera spp.* This area has a sub-arctic climate with short, cool, wet summers and long, cold winters.

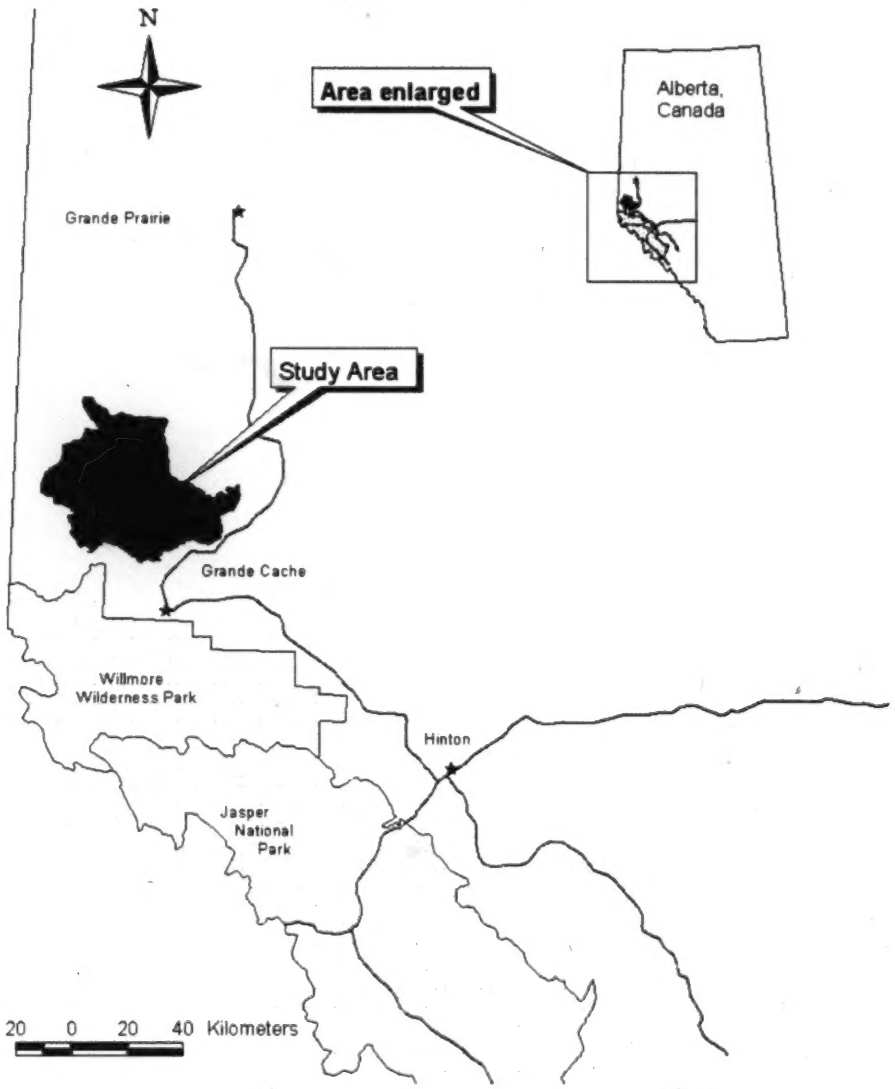


Figure 2-1. Map of the study area, which encompasses the Redrock/Prairie Creek caribou winter range, in west central Alberta.

Caribou Location Data

As part of a larger study in west central Alberta, GPS (Global Positioning System) collars were deployed on 20 adult female caribou over three winters. Only one caribou was collared over two consecutive years. Five caribou were collared for the winter of 1998/99, and eight caribou were collared for the winters of 1999/00 and 2000/01, for a total of 21 caribou-years. Caribou were captured by net gunning, while in open alpine areas. The captures met standards required for animal care, and were approved by the University of Alberta Faculty of Agriculture, Forestry and Home Economics (Protocol No. 99-75D). GPS collar data collected in 1998/99 could not be differentially corrected and were therefore only accurate within 100 m, 95% of the time (Lotek Engineering Inc. 2000). However, data from 1999/00 and 2000/01 were corrected, and were therefore accurate within 14 m, 95% of the time (Lotek Engineering Inc. 2000). Data were corrected using Lotek Engineering software (N-4 Version 1.1895, 2000) and relatively inaccurate locations, identified by a Degree of Precision value greater than 12, were removed.

GPS collars were scheduled to collect data between four and 24 times per day. To increase the independence among locations and ensure sampling at constant intervals, I selected one location per day (1200hrs when available, or 1000hrs otherwise) for most statistical analyses. Winter locations (December 1st - May 1st) were selected, resulting in 11-150 locations per caribou-year (Table 2-1). Due to collar dysfunction, location data for some animals were very sporadic (Figure 2-2), and one caribou-year (16) did not collect any locations within the winter range.

Table 2-1. Number of daily GPS caribou locations collected over three winters (December 1998 - March 2001) for the Redrock/Prairie Creek caribou. Locations were taken at 1200hrs when available, or 1000hrs otherwise. Note that caribou-years 4 and 13 represent the same individual caribou during different years of the study. No other caribou were collared during multiple years.

Year	Caribou-Year	Number of locations
1998/99	1	150
	2	84
	3	135
	4	143
	5	135
1999/00	6	38
	7	69
	8	122
	9	123
	10	124
	11	140
	12	126
	13	138
2000/01	14	101
	15	96
	16	29
	17	100
	18	11
	19	78
	20	100
	21	99
Total		**2141**

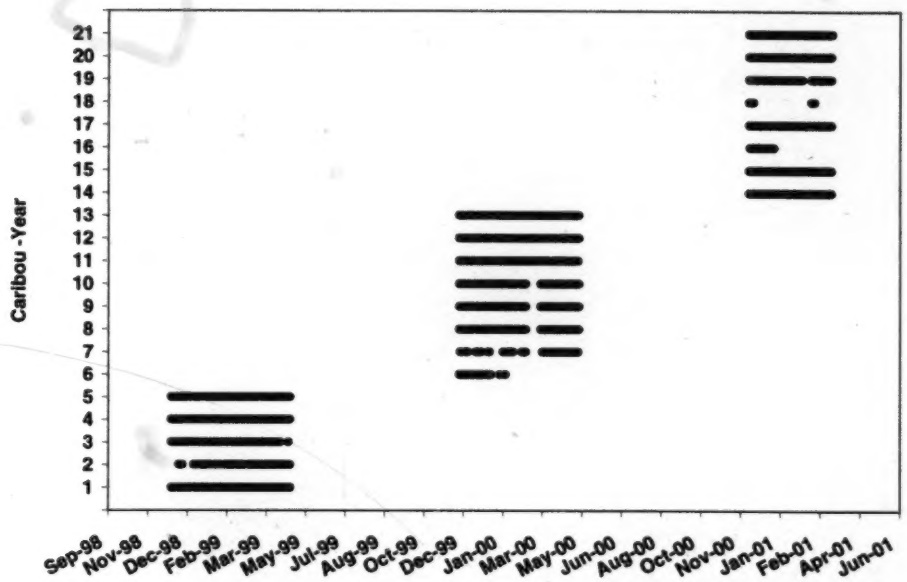


Figure 2-2. Dates with GPS locations for each caribou-year in the Redrock/Prairie Creek range from December 1998 - March 2001. One location per day was selected (at 1200hrs when available, or 1000hrs otherwise).

GIS Methods

Habitat selection was analysed at two spatial scales. At the coarse scale, I analysed home range selection within the study area. For the fine scale, I analysed selection for general habitat use within each caribou's home range. The coarse scale was a design 2 study (Thomas and Taylor 1990), since available habitat was the same for all animals, while used habitat was unique for each animal. The fine scale was a design 3 study, since used *and* available habitats were unique for each animal.

To obtain forest stand information associated with each caribou location, I overlaid caribou locations on digital Phase 3 forest mapping (from Weyerhaeuser Company Ltd.), using ArcView GIS (Geographic Information System) software (Version 3.1, Environmental Systems Research Institute Inc. 1993). Phase 3 mapping consists of polygons delineated through air photo interpretation, and contains information on overstory forest attributes, and stand ages (Alberta Forest Service 1984). Since Phase 3 mapping was only available for "productive" stands (i.e. stands with a density greater than 6% and cutblocks), habitat selection analyses were restricted to these stands. I updated Phase 3 using timber harvesting information from 2000 (the most up-to-date information available). Cutblocks were re-aged, according to harvest date, and a value of 0 was assigned to stand density, and percent pine and spruce (which is consistent with Phase 3 classification).

I defined each caribou's winter home range by a 2.8 km buffer around daily caribou locations, which represented the 90th percentile of the daily distance travelled by caribou during the winter, averaged across all caribou. Others have also used a

percentile of daily travel distances to define used or available habitat (Servheen and Lyon 1989; Maehr and Cox 1995; Apps and Kinley 2000; Rettie and Messier 2000; Apps et al. 2001; Oberg 2001). The buffered area represents habitat that is reasonably accessible to each caribou throughout the winter. Traditional home range delineators such as Minimum Convex Polygons do not adequately represent caribou home ranges, as caribou do not establish a true home range, and instead move nomadically through the landscape (Figure 2-3).

To obtain information on forest stands within each caribou's home range, I buffered each caribou location (Figure 2-4), created 100 random points within these buffers (using Animal Movement Analyst ArcView extension; Alaska Biological Science Centre), overlayed the random points on Phase 3, and determined the forest stands associated with each point. Random points provided the binary data required for logistic regressions, and were translated into proportions for compositional analyses (see below). In some instances, however, the 100 random points were insufficient to detect rare forest stand categories (i.e. stand categories that made up < 1% of a home range). Since zero values are problematic for compositional analyses (Aebischer et al. 1993), I used an alternate method to determine habitat availability for caribou home ranges with missing values. This involved overlaying caribou home ranges on Phase 3, and using the outer edges of these ranges to "clip" out Phase 3 information (like a cookie cutter). Then, the "clipped" information was pulled into a table and the proportion of each habitat category available was calculated. Since all habitat polygons within the caribou home range were "clipped", even rare habitat categories were detected, and could be used in analyses.

Information on available habitat in the Redrock/Prairie Creek study area was obtained by creating 1000 random points across the study area and overlaying these points on Phase 3 forest inventory data. The study area was delineated based on the Minimum Convex Polygon of caribou locations from 1981 to 1996 (Alberta Sustainable Resource Development, Grande Prairie, unpubl. data).

Statistical Analyses

There are many approaches for analysing habitat selection. Logistic regression is useful because the relative importance of many variables may be analysed, and continuous data may be used (Menard 1995; Alldredge et al. 1998; Boyce and McDonald 1999). Since animals may select habitats for several attributes, it is important to analyse habitat variables simultaneously (Porter and Church 1978). Other advanced methods, such as moving window analyses (Arthur et al. 1996) and compositional analyses (Aebischer et al. 1993), are advantageous because serial autocorrelation assumptions can be relaxed, and the level of analysis is more appropriate (because each caribou, rather than each location, is a datum). However, these methods require categorical data, and it is onerous to analyse all possible combinations of habitat variables. Although continuous data can be converted into categories, arbitrary divisions must be made in defining categories, which may influence results (Johnson 1980). To combine the benefits of both types of methods, I first used multiple logistic regression to explore pooled data and aid in defining important variables and break points. Then, I used compositional analysis to address concerns with autocorrelation and level of analysis (Aebischer et al. 1993).

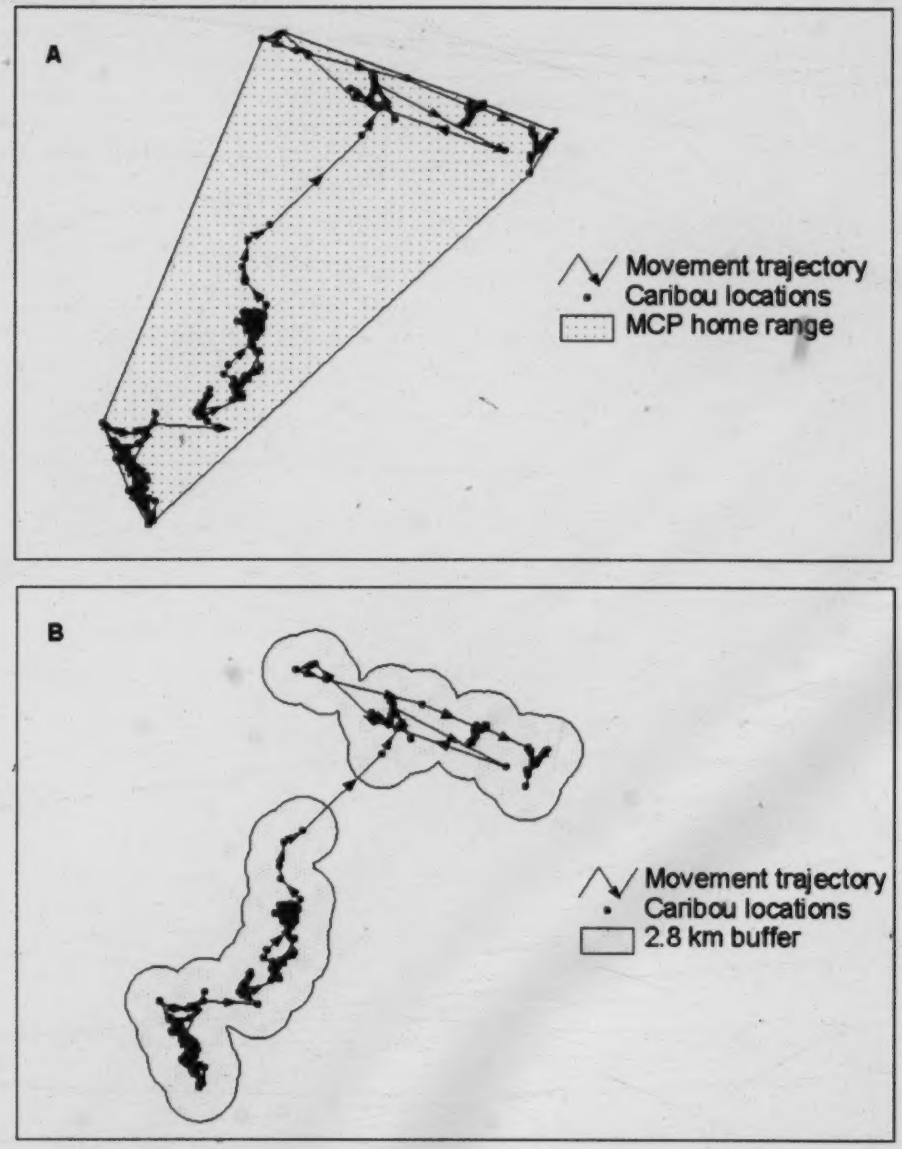


Figure 2-3. Comparison of home range techniques, showing the Minimum Convex Polygon (MCP) method commonly used for species with true home ranges (**A**) and the buffer method used for my analyses (**B**). The 2.8 km buffer represents the 90th percentile of daily movement distances.

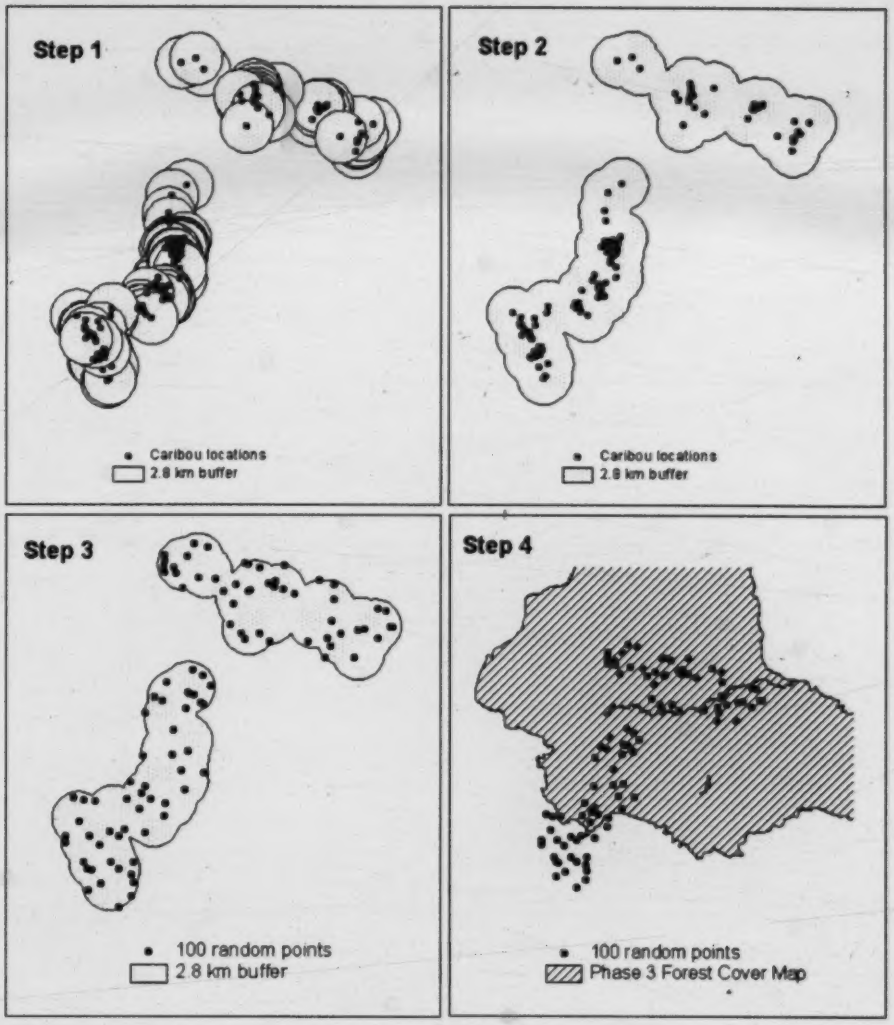


Figure 2-4. Steps for determining forest stands available within each caribou's home range. For each caribou I: 1) buffered caribou locations, 2) dissolved the boundaries of the buffers to create one contiguous buffer, 3) created 100 random points in the buffer and 4) overlayed the random points on the Phase 3 map to determine forest stand characteristics associated with each point.

Exploratory Analyses

For all multiple logistic regression analyses, I tested for collinearity using tolerance statistics and for non-linearity using the Box-Tidwell test (Menard 1995). Studentized residual, leverage and dbeta diagnostics were calculated and investigated for outliers (Menard 1995). I combined used and available forest stand information (for all caribou across all years) into a single file and created a dummy variable to identify points associated with used habitat (value of one) and available habitat (value of zero). Forest stand information included percentage of lodgepole pine and white spruce, stand age (years) and stand density (% canopy closure). Stand density values from Phase 3 were expressed as ranges, and were converted to the midpoint for analyses.

I analysed the significance of the overall model and individual variables using drop in deviance analyses (Menard 1995). These involve comparing models with and without the variables being tested, to calculate a chi-squared test statistic. Since p-values may be deflated because of extremely large sample sizes (each caribou location was a datum, rather than each caribou) (Maehr and Cox 1995), I used t-tests and compositional analyses to corroborate my findings. T-tests compared the mean of individual habitat variables for used locations, to available locations. The most parsimonious model was used to produce line graphs showing the relationship between habitat preference (expressed as relative predicted probability of habitat use) and individual habitat variables. When models had more than one significant variable, I plotted individual variables by substituting the mean value for other significant variables in the model. The odds ratio, calculated by Exp(B) – 1 from

SPSS (Version 9.0, SPSS Inc. 1998) output, indicates the percent change in the probability of habitat use, associated with a 1% change in the habitat variable.

Compositional Analyses

I analysed significant variables from logistic regression analyses using compositional analysis. If habitat use was significantly non-random (Aebischer et al. 1993), I determined which habitats were selected over other habitats by calculating differences in log ratios. This was calculated for each pair of habitat categories, for each caribou individually, by:

$$\ln(u_i / u_j) - \ln(a_i / a_j),$$

where u_i and u_j are the proportion of used habitat for categories *i* and *j*, and a_i and a_j are the proportion of available habitat for categories *i* and *j*. Then, I calculated the mean and standard error for these pair-wise comparisons across all caribou, and tested for significance using a student's t-test.

In some instances, a habitat category was available, but not used by an individual. In these cases I replaced the 0 value for used habitat with 0.001, which is an order of magnitude less than the smallest recorded nonzero proportion (Aebischer et al. 1993). I considered a habitat to be preferred or avoided relative to another habitat if the p-value was less than 0.10. However p-values between 0.05 and 0.10 were considered to have only weak evidence of preference or avoidance, and are discussed accordingly.

Seasonal Analyses

I analysed habitat selection at finer temporal scales because habitats may change over time (e.g., as snow conditions change), and habitat selection patterns

may change accordingly (Arthur et al. 1996). Habitat selection was analysed for early winter (January 1 to 31) and late winter (March 1 to 31) at both coarse and fine scales. Compositional analyses were used to analyse habitat selection patterns for spruce and/or age, when these variables were significant for the entire winter.

Temporal Analyses

To ensure that the locations selected for my analyses (1200hrs when available, or 1000hrs otherwise) were representative of habitat selection across all times of day, I performed a chi-squared analysis to compare fine scale habitat use by caribou during 4-hour time periods (0200-0600hrs, 0600-1000hrs, 1000-1400hrs, 1400-1800hrs, 1800-2200hrs, and 2200-0200hrs). This analysis was conducted for those habitat variables found to be significant for fine-scale compositional analyses.

Annual Analyses

Since habitat selection may differ substantially among years (Schooley 1994), I performed a chi-squared analysis to compare fine scale habitat use by caribou during the three years of my study, for those habitat variables found to be significant in the fine-scale compositional analyses. In addition, to visualise differences in selection (use compared to availability), I plotted habitat use as a proportion of expected use, for each year separately.

Caribou Independence

The statistical tests performed have an underlying assumption that each animal represents an independent measure of habitat choice (Aebischer et al. 1993). Oberg (2001), using the same caribou location data for 1998/99 and 1999/00, concluded that caribou travelling in the same group might have violated this

assumption. Caribou were considered to be travelling together if their locations were less than 1 km apart. I augmented Oberg's (2001) results by analysing caribou data from 2000/01, following an identical approach. I selected 19 days, roughly one week apart, when locations were available for all, or most, caribou. Then, I calculated the distance between every pair of caribou, and determined the percent of locations, for each pair, that were less than 1 km apart.

RESULTS

Exploratory Analyses

At the coarse scale, caribou used stands with a mean age of 111 years, while available stands had a mean age of 104 years ($t = -4.073$, $df = 2254$, 1-sided $p < 0.001$). Stands used by caribou had a mean canopy closure of 61% compared to 57% for available stands ($t = -4.497$, $df = 2254$, 1-sided $p < 0.001$). The percent of pine was 61% for stands used by caribou and 59% for available stands ($t = -1.289$, $df = 2254$, 1-sided $p = 0.099$), and the percent of spruce in stands used by caribou was 24% compared to 21% in stands available to caribou ($t = -2.702$, $df = 2254$, 1-sided $p = 0.004$). Multiple logistic regression indicated that age, density and spruce were significant variables at the coarse scale (Table 2-2, Figure 2-5). Since the model also indicated non-linear forms for stand age (Box-Tidwell test, chi-squared = 6.553, $df = 1$, $p = 0.010$), and stand density (Box-Tidwell test, chi-squared = 20.278, $df = 1$, $p < 0.001$) the variables **(age)ln(age)**, and **(density)ln(density)** were retained in the final model. Habitat preference (relative predicted probability of habitat use) first declined, and then increased, with canopy closure (density), and increased with

percent of spruce. There was a general increase in preference for older stands until about 150 years, when preference declined slightly. 59.31% of the points were correctly classified as used or available, and 1.74% of the variation between used and available habitats was accounted for by the model. The odds ratios listed in logistic regression tables indicate the percent change in the probability of habitat use, associated with a 1% change in the habitat variable.

At the fine scale, caribou used stands that were older, denser, and had a higher percent of pine, than expected. The mean age of used habitat was 127 years, while available habitat was 112 years ($t = -9.136$, $df = 2563$, 1-sided $p < 0.001$). Used habitat had a mean canopy closure of 65%, while available habitat was 61% ($t = -6.106$, $df = 2563$, 1-sided $p < 0.001$). The mean percent of pine at used stands was 65%, while available habitat was 61% ($t = -2.801$, $df = 2563$, 1-sided $p = 0.003$). Mean percent spruce was similar for used and available stands (24% for both; $t = 0.302$, $df = 2563$, 1-sided $p = 0.381$). Multiple logistic regression identified stand age, density and percent spruce as significant predictors of fine scale caribou habitat selection (Table 2-3, Figure 2-6). 58.99% of the caribou locations were correctly classified as used or available and the model accounted for 3.32% of the variation between used and available habitat. The Studentized residual recognised three potential outliers (values >2, but still <3). These values were checked, and although unusual (used cutblocks), they were not removed from the analyses. Both fine and coarse scale models had evidence of a lack-of-fit (Hosmer-Lemeshow, coarse scale: chi-squared = 29.9, $df = 8$, $p < 0.001$; fine scale: chi-squared = 38.9, $df = 8$, $p < 0.001$).

Table 2-2. Coarse scale logistic regression model describing the forest stand characteristics important for habitat selection by caribou wintering in west central Alberta from December 1998 – March 2001. P-values for habitat variables were calculated using a drop in deviance test, while the p-value for the constant variable was from a Wald's test.

Habitat selection				
(n = 2256, model chi-squared = 53.024, df = 5, p < 0.001)				
Variables retained in the model	**B**	**SE**	**p**	**Odds Ratio**
Age	0.059	0.022	0.007	6.05%
(Age)ln(age)	-0.010	0.004	0.010	-0.97%
Density	-0.126	0.030	0.000	-11.84%
(Density)ln(density)	0.028	0.006	0.000	2.82%
Percent Spruce	0.006	0.002	0.000	0.06%
Constant	-0.460	0.252	0.068	
Variables removed from the model				
Percent Pine	-	-	0.372	-

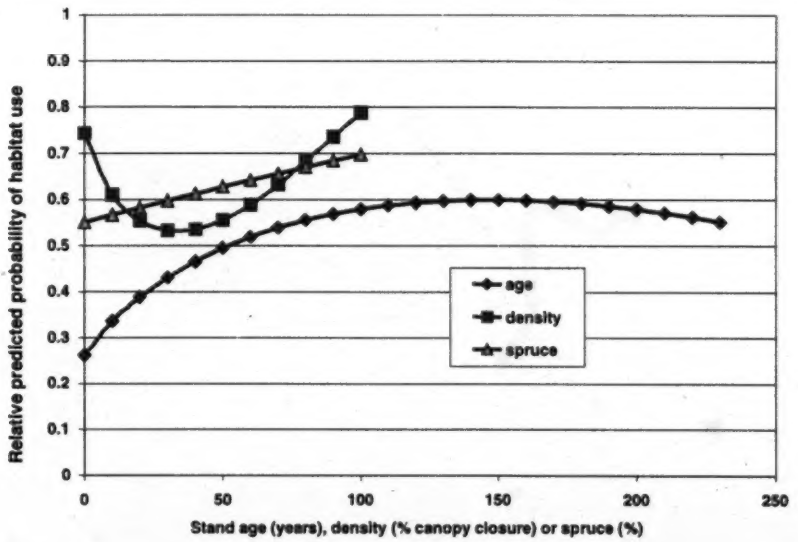


Figure 2-5. Coarse scale relative predicted probability of habitat use relative to stand age, density and percentage of spruce in a stand, for caribou wintering in west central Alberta (December 1998 – March 2001).

Table 2-3. Fine scale logistic regression model describing the forest stand characteristics important for habitat selection by caribou wintering in west central Alberta from December 1998 – March 2001. P-values for habitat variables were calculated using a drop in deviance test, while the p-value for the constant variable was from a Wald's test.

Habitat selection				
(n = 2565, model chi-squared = 133.461, df = 4, p < 0.001)				
Variables retained in the model	**B**	**SE**	**p**	**Odds Ratio**
Age	0.009	0.001	0.000	0.93%
Density	0.131	0.042	0.001	0.58%
(Density)ln(density)	-0.024	0.008	0.001	14.04%
Percent Spruce	-0.006	0.002	0.001	0.58%
Constant	-2.940	0.464	0.000	
Variables removed from the model				
Percent Pine	-	-	0.765	-

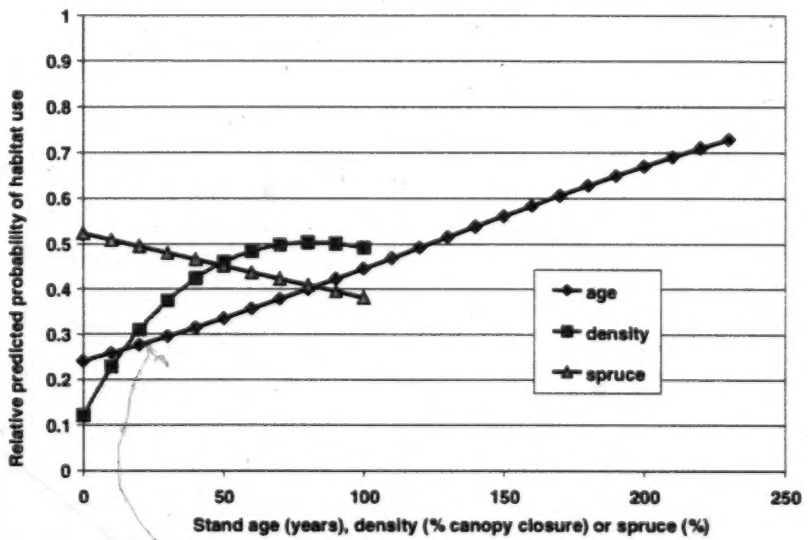


Figure 2-6. Fine scale relative predicted probability of habitat use relative to stand age, density and percentage of spruce in a stand, for caribou wintering in west central Alberta (December 1998 – March 2001).

Compositional Analyses

Compositional analyses were conducted following the logistic regression analyses, in part because these analyses do not require location data to be independent. There was some evidence that auto-correlation was present in the data, as 5.4 – 45.7% (mean = 19.6% per animal) of daily individual caribou locations were in the same forest polygon as the previous day.

At the coarse scale, I conducted compositional analyses for stand age, density and percent spruce, and at the fine scale, I analysed selection for stand age and density. These variables were chosen based on results from logistic regression analyses, and t-tests comparing the mean for used habitat to available habitat. For example, although spruce was a significant variable in the fine scale logistic regression, this variable was not analysed using compositional analyses because the t-test comparing spruce in used and available habitat was not significant. Bar graphs depicting mean habitat use, as a proportion of expected use (i.e. available habitat), are shown for all significant compositional analyses. On these graphs, solid horizontal lines show which habitat categories were not significantly different from each other (at $p < 0.10$). If no horizontal lines are shown, all habitat categories are significantly different from each other.

At the coarse scale, caribou selected habitats based on stand age (chi-squared = 9.58, df = 4, $p = 0.048$), and density (chi-squared = 29.92, df = 4, $p < 0.001$), but not spruce (chi-squared = 7.224, df = 4, $p = 0.125$). Caribou avoided stands under 80 years relative to the most preferred stands, which were 120-160 years (0-40 years: t =

2.600, df = 19, 1-sided p = 0.009; 40-80 years: t = 2.114, df = 19, 1-sided p = 0.024) (Figure 2-7). As with the logistic regression analysis, preference declined slightly for the oldest stands. All stand categories were avoided relative to the densest stands (71-100%), which were most preferred (<6%: t = 4.588, df = 19, 1-sided p < 0.001; 6-30%: t = 3.878, df = 19, 1-sided p = 0.001; 31-50%: t = 2.656, df = 19, 1-sided p = 0.008; 51-70%: t = 1.909, df = 19, 1-sided p = 0.036). As with the logistic regression, there was a slight increase in use for stands with <6% canopy closure, although this category was not significantly preferred relative to the 6-30% category.

At the fine scale, caribou habitat selection was significantly different from random for age (chi-squared = 18.81, df = 4, p = 0.001) and density (chi-squared = 19.87, df = 3, p < 0.001). Caribou avoided stands under 120 years old relative to stands over 160 years, which were most preferred (0-40 years: t = 7.228, df = 19, 1-sided p < 0.001; 40-80 years: t = 3.686, df = 19, 1-sided p = 0.001; 80-120 years: t = 2.834, df = 19, 1-sided p = 0.005) (Figure 2-8). I merged stand density categories <6% and 6-30%, because of a lack of availability of these stands for many animals (Aebischer et al. 1993). The densest stand category, 71-100% canopy closure, was the most preferred, and the most open category was relatively avoided (0-30%: t = 7.498, df = 19, 1-sided p < 0.001). However, other categories were not relatively avoided (31-50%: t = 1.302, df = 19, 1-sided p = 0.104; 51-70%: t = 0.931, df = 19, 1-sided p = 0.182).

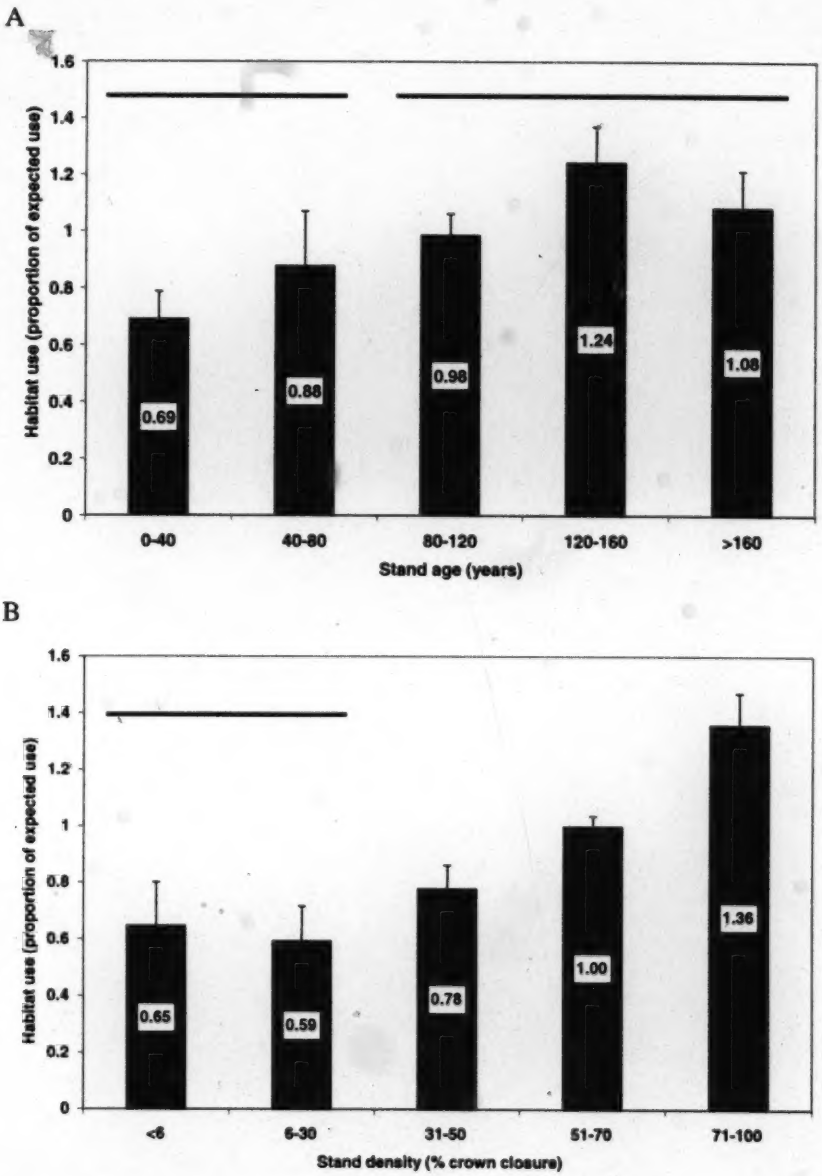


Figure 2-7. Coarse scale habitat selection by caribou wintering in west central Alberta (December 1998 – March 2001) for stand age (**A**) and stand density (**B**). Solid horizontal lines show which categories are not significantly different (at $p = 0.10$). Error bars show ± 1 SE.

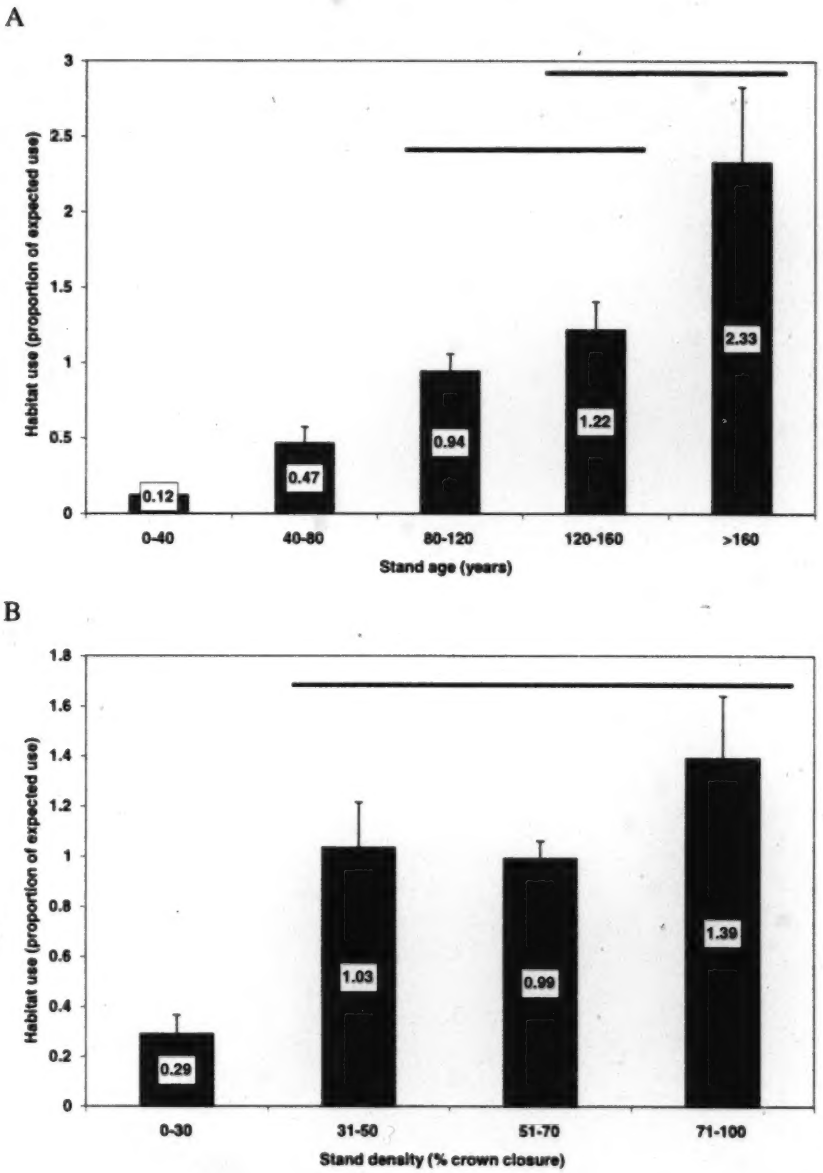


Figure 2-8. Fine scale habitat selection for stand age (**A**) and stand density (**B**), by caribou wintering in west central Alberta (December 1998 - March 2001). Solid horizontal lines show which categories are not significantly different (at $p = 0.10$). Error bars show ± 1 SE.

Seasonal Analyses

Habitat selection was analysed separately for early winter (January 1-31) and late winter (March 1-31) at the fine and coarse scales. Selection patterns differed between the two periods (Figure 2-9 and Figure 2-10). At both scales, the youngest age category was used (relative to expected use) much less in the late winter than in the early winter (0.29 compared to 0.68 at the coarse scale, and 0.09 compared to 0.24 at the fine scale). Also, older stands were used proportionately more in the late winter than in the early winter at both scales.

At the coarse scale, in the early winter, the two youngest stand age categories were significantly avoided relative to stands over 160 years, which were most preferred (0-40 years: $t = 2.580$, $df = 16$, 1-sided $p = 0.010$; 40-80 years: $t = 4.079$, $df = 16$, 1-sided $p < 0.001$). In the late winter, all stand age categories were significantly avoided relative to the oldest stand age category (0-40 years: $t = 5.774$, $df = 17$, 1-sided $p < 0.001$; 40-80 years: $t = 3.786$, $df = 17$, 1-sided $p < 0.001$; 80-120 years: $t = 4.117$, $df = 17$, 1-sided $p < 0.001$; 120-160 years: $t = 2.302$, $df = 17$, $p = 0.017$).

At the fine scale, in early winter, caribou avoided stands under 80 years old relative to 80-120 year old stands, which were most preferred (0-40 years: $t = 2.916$, $df = 13$, 1-sided $p = 0.006$; 40-80 years: $t = 2.334$, $df = 13$, 1-sided $p = 0.018$). In the late winter, caribou avoided stands under 80 years as well. However, stands over 160 years were most preferred, and results are therefore compared to this category (0-40 years: $t = 2.290$, $df = 10$, 1-sided $p = 0.023$; 40-80 years: $t = 3.856$, $df = 13$, 1-sided $p = 0.001$).

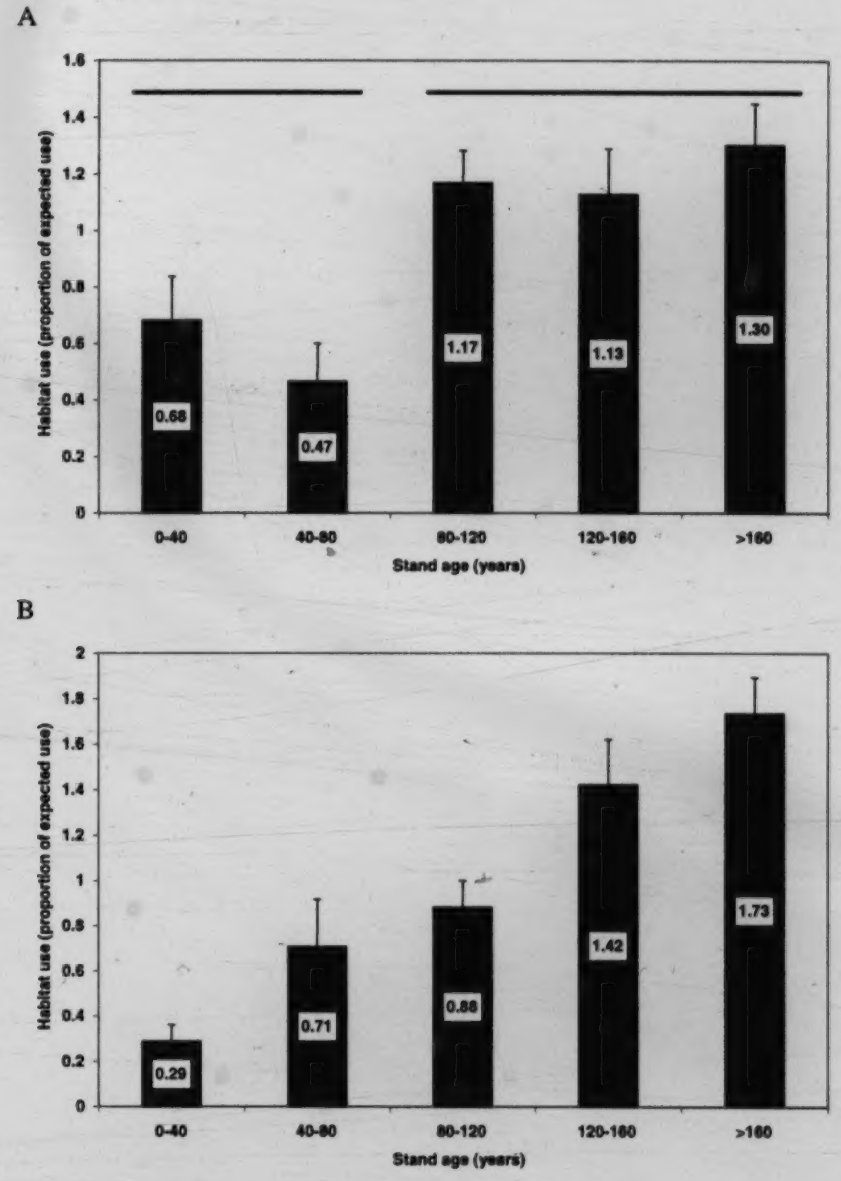
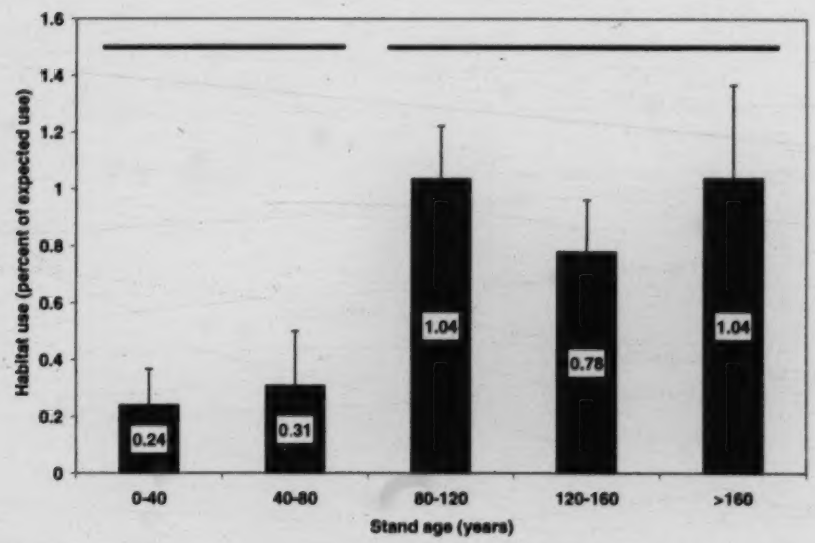


Figure 2-9. Coarse scale habitat selection for stand age by wintering caribou in west central Alberta (December 1998 – March 2001) in the early winter (**A**) and late winter (**B**). Solid horizontal lines show which categories are not significantly different (at $p = 0.10$). Error bars show ± 1 SE.

A



B

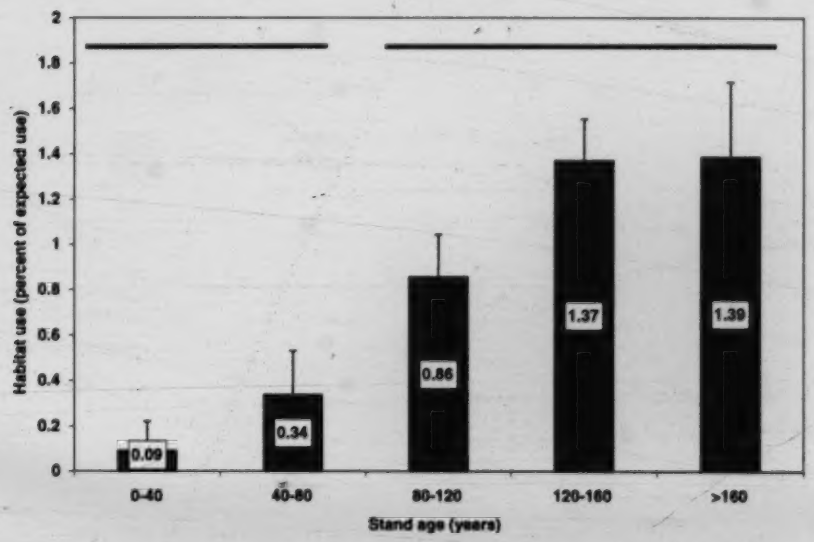


Figure 2-10. Fine scale habitat selection for stand age by wintering caribou in west central Alberta (December 1998 – March 2001) in the early winter (**A**) and late winter (**B**). Solid horizontal lines show which categories are not significantly different (at $p = 0.10$). Error bars show ± 1 SE.

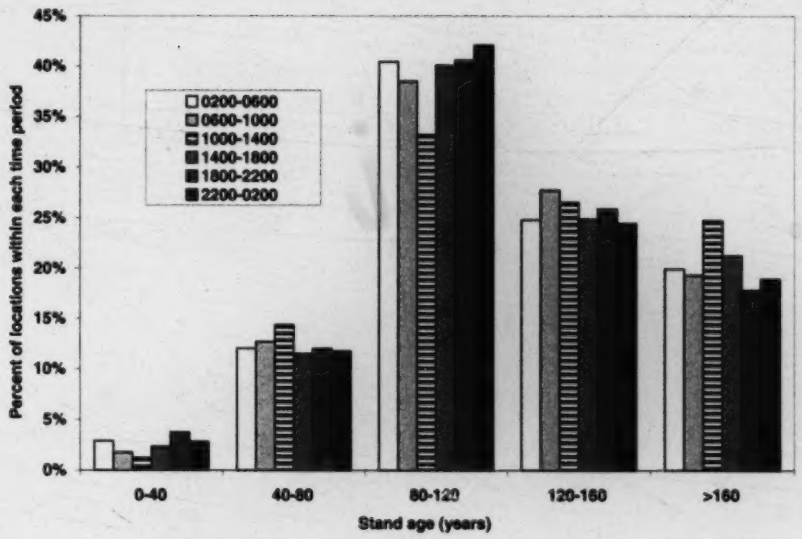
Temporal Analyses

Caribou habitat use of stand age differed significantly among time periods (chi-squared = 206.6, df = 20, $p < 0.001$). If caribou used habitats consistently throughout the day, the percent of caribou locations in each time period would be the same within each age and density category (Figure 2-11). The time period analysed in my study (1000–1400hrs) may have slightly over-represented habitat use for stands 40-80 years old and over 160 years, while habitat use of stands 80-120 years may have been under-represented. There was also significantly different use of stand density among time periods (chi-squared =39.40, df = 20, $p = 0.006$). Figure 2-11 shows the 1000hrs–1400hrs time period may slightly over-represent the 51-70% density category, while under-representing the 71-100% category. However, the overall trend for age and density was similar, regardless of the time period.

Annual Analyses

Habitat use at the fine scale differed among years for both age (chi-squared = 65.93, df = 8, $p < 0.001$), and density (chi-squared = 56.868, df = 8, $p < 0.001$). Figure 2-12 shows a difference in selection (use relative to expected use) as well, for both age and density. For stand age, the trend of increasing preference for older stands was consistent among years, although the strength of this trend differs, and was least pronounced for 2000/01. For density, the most open stands (0-30% canopy closure) were consistently used the least, relative to the other categories, while the most preferred density category differed among years (71-100% for 1998/99 and 2000/01, and 51-70% for 1999/00).

A



B

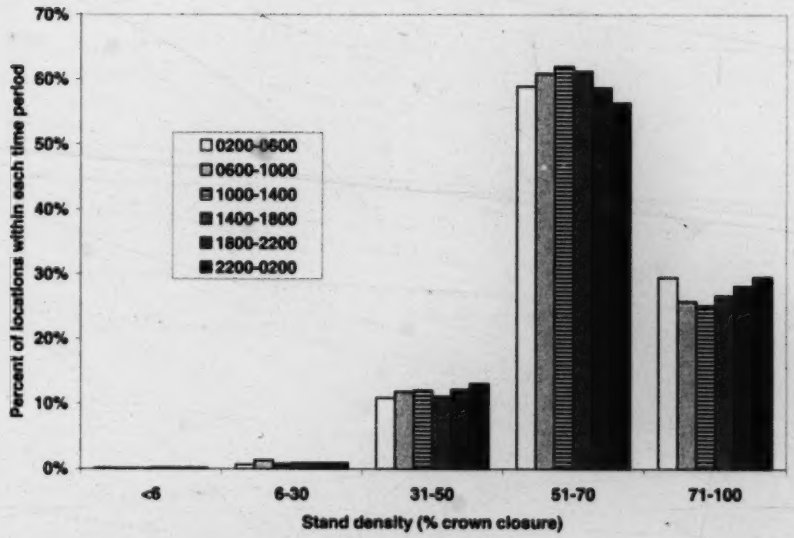
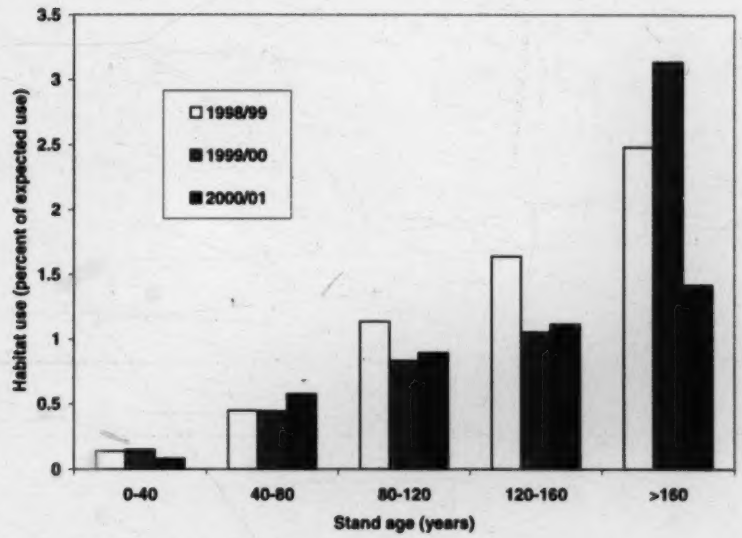


Figure 2-11. Fine scale habitat use by caribou wintering in west central Alberta (December 1998 – March 2001) at 4-hour time periods. Values are the percent of caribou locations in each time period in each stand age (**A**) or density (**B**) category.

A



B

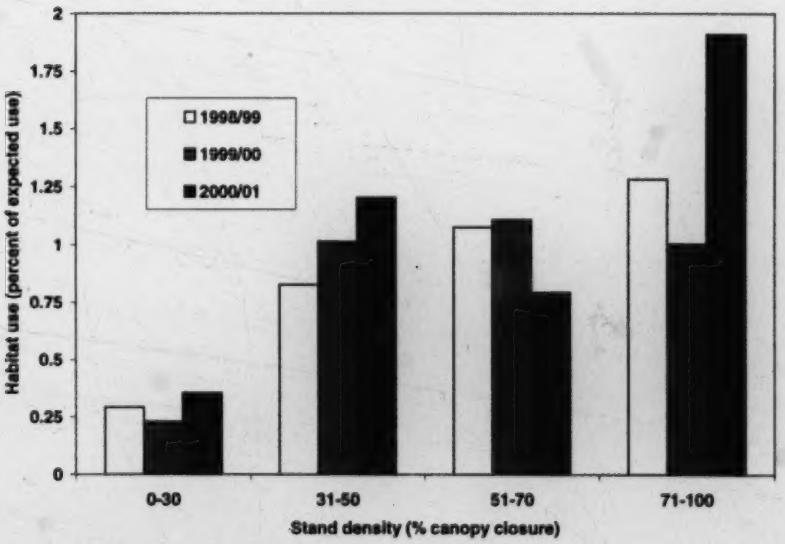


Figure 2-12. Fine scale habitat use of stand age (**A**) and density (**B**), for caribou wintering in west central Alberta, December 1998 – March 2001. Values are expressed as a proportion of expected use, for each year separately, to highlight variability among years.

Caribou Independence

During 2000/01, none of the caribou travelled together for the entire winter. However, there was evidence of a lack of independence between some pairs of caribou (Table 2-4). One pair of caribou (caribou-years 14 and 17) were within 1 km of each other for 47.4% of the 19 analysed days. Four additional pairs of caribou spent between 10.5-16.7% of the time in close proximity to each other (less than 1 km). The remaining 23 pairs of caribou were entirely independent over the winter.

Table 2-4. Percent of locations within 1 km of each other, for each pair of caribou over the winter of 2000/01, in west central Alberta.

Caribou-Year	14	15	16	17	18	19	20	21
14		10.5%	0.0%	47.4%	0.0%	16.7%	0.0%	0.0%
15			0.0%	0.0%	0.0%	0.0%	15.8%	0.0%
16				0.0%	0.0%	0.0%	0.0%	0.0%
17					0.0%	0.0%	10.5%	0.0%
18						0.0%	0.0%	0.0%
19							0.0%	0.0%
20								0.0%
21								

DISCUSSION

My research differs from past caribou research in the Redrock/Prairie Creek range in three main ways. First, I analysed habitat selection (which compares use to availability), while earlier studies reported habitat use (Edmonds and Bloomfield 1984). Second, past research relied on snow-tracking (Stepaniuk 1997) or VHF (Very High Frequency) telemetry locations (Bjorge 1984; Edmonds and Bloomfield 1984), which lack the sample size and accuracy of the relatively new technologies used in my study (GPS collars and GIS computer mapping). Third, my research was conducted at two spatial scales, and attempts to discern differences in habitat

selection within the winter (i.e., in early and late winter). These methods provide a greater understanding of the habitat requirements of woodland caribou in this area.

Habitat studies should analyse selection at multiple spatial scales, because selection may differ among scales (e.g., Wiens 1989; Apps and Kinley 2000; Schneider et al. 2000), and findings may depend on how availability is defined (Johnson 1980; Arthur et al. 1996). In addition, habitat selection at coarser scales may negate selection at finer scales (Johnson 1980; Thomas and Taylor 1990). For instance, if an animal selects pine forests at a coarse (e.g., home range) scale, then pine will be abundant throughout the animal's home range. Subsequent analyses for selection at finer scales (e.g., within the home range) may therefore not identify selection for pine. Thus, an analysis restricted to the finer scale would lead to the misleading conclusion that the animal does not prefer pine forest.

My predictions for caribou habitat selection were similar for both fine and coarse scales, presumably because many habitats used by caribou meet both their forage and predator-avoidance requirements (Rettie and Messier 2000). For instance, caribou may avoid predators by inhabiting older forests (which often have abundant lichens), because alternate prey are generally not abundant in these habitats. This anti-predator strategy may have driven the caribou's adaptation to lichen foraging, and thus predator avoidance and forage selection may be intrinsically linked. Although I attempt to interpret my results in terms of selection for predator avoidance or forage, these are not clearly distinguishable in many instances.

Coarse Scale Habitat Selection

Although the compositional analyses showed strong selection by caribou for several habitat variables (and these variables were found to be significant in the logistic regression analyses), quantitative evaluation of the logistic regression model indicated a poor fit to the data (i.e. evidence of a lack of fit and low percent variation accounted for by the model). The extremely large sample sizes for both the coarse and fine scale analyses (n = 2256 and 2565, respectively), contributed to significant models, but high variance in the data resulted in poor fit. Also, as previously discussed, there are several additional concerns with logistic regression analyses, including inappropriate data pooling and auto-correlation. Thus, greater emphasis is placed on the compositional analyses when interpreting my results.

I determined which habitat characteristics, within the larger study area, caribou selected for their home ranges. I found that caribou generally preferred older stands with the highest preference for 120-160 year old stands. A slight decline in preference was observed for stands over 160 years. Similarly, others have found that caribou avoid young stands created through timber harvesting (Cumming and Beange 1993; Smith et al. 2000). These findings are consistent with the prediction that caribou avoid young forests at the coarse scale, presumably to reduce their proximity to alternate prey species (Schwartz and Franzmann 1989) and, in turn, predators (Cumming 1992). The 40 year old stand age may be particularly significant, since moose densities, which increase following disturbances such as fire, have been found to return to pre-disturbance levels after about 40 years (Schwartz and Franzmann 1989).

Caribou also showed the greatest preference for stands with 70-100% canopy closure, with a relative avoidance of all other density categories. This, again, may be attributed to predator avoidance. Although semi-open stands improve growing conditions for lichens, more open stands with sufficient moisture may allow for greater shrub growth, which provides prime habitat for alternate prey such as moose (Telfer 1978; Racey et al. 1991), and subsequently wolves. In fact, selection for dense stands may be even greater than my findings indicate, as the GPS collars used to collect location data on caribou are less likely to obtain a position when under dense canopies (Remple et al. 1995). Although, according to the compositional analysis, the most open stands (<6% crown closure, which largely represent cutblocks and burns) were avoided relative to denser stands, the logistic regression model showed an increase in preference for these stands. This may simply be due to problems associated with logistic regression (as discussed previously), or may be attributed to traditional use of the range. Rettie and Messier (2000) found that some populations of woodland caribou selected cutblocks and burns at a coarser scale, but avoided these habitats at finer scales. They speculated that the coarse scale represented traditional habitat use, rather than current selection, and that there would be a lag before caribou would respond to these disturbances within their range.

Finally, there was some evidence (from logistic regression, but not compositional analysis) that caribou preferred stands with a higher percent of spruce. Although I found that caribou did not select spruce stands at the fine scale, caribou may select spruce within their home range to ensure that these stands are close by, if required. Thomas et al. (1996) speculated that caribou might ensure that stands with

abundant arboreal lichens are nearby, in case harsh snow conditions force caribou to rely temporarily on arboreal lichens, and travel to distant habitats is difficult (Stardom 1975). In my study area, arboreal lichen biomass increased with the percent of spruce in a stand (Chapter 3).

Fine Scale Habitat Selection

Caribou avoided stands under 120 years old relative to stands over 160 years, which were strongly preferred. Unlike the coarse scale, there was no plateau in the logistic regression function; preference continued to increase for the oldest stands. Bjorge (1984) also found that caribou in this area avoided stands less than 82 years, and selected stands 122-141 years and greater than 162 years. Slight differences in results may be attributed to Bjorge's (1984) differences in sampling (i.e. VHF telemetry), and/or his definition of available habitat, which was the entire study area, rather than home ranges as in my fine scale analysis. Preference for older stands may be attributed to forage selection, to predator and alternate prey avoidance (as previously discussed), or to some combination of the two. Terrestrial and arboreal lichens are generally more abundant in older stands (Ahti and Hepburn 1967; Edmonds and Bloomfield 1984; Thomas et al. 1996; Rettie et al. 1997), and thus my findings are consistent with the hypothesis that caribou select habitats for forage at this scale.

Denser stands were selected at the fine scale, and caribou used stands with a mean canopy closure of 65.2%. This may differ somewhat from Bjorge (1984), who found selection for "medium" density stands and avoidance of "sparse" stands.

Although his results are difficult to compare directly to mine (as density categories were not defined in terms of percent canopy closure), my results suggest a selection for relatively denser stands than previously found. I predicted that caribou would select more open stands at this scale, since terrestrial lichens are more abundant in semi-open stands (Edmonds and Bloomfield 1984; Thomas et al. 1996). There are two possible explanations for this deviation. First, caribou may be selecting dense stands because of greater snow interception (Golding and Swanson 1978), which reduces the effort required for travelling and cratering (Henshaw 1968; Thing 1977; Skogland 1978; Fancy and White 1985). Second, even this fine spatial scale may be too coarse to adequately represent habitat selection for forage. Others have suggested that animals select habitats to address their most important limiting factor (i.e. predation, in the case of caribou) at the coarsest scale. If they are unsuccessful at meeting their needs at this scale, they will continue to select for the required habitat attributes at successively finer scales (Rettie and Messier 2000). Therefore, caribou may still be selecting habitats for predator avoidance at this fine scale, with habitat selection for foraging operating at an even finer scale. In Chapter 3, I found that caribou selected moderately dense stands (around 50% canopy closure) for cratering, which corresponds more closely with my forage selection prediction. Also, caribou may be foraging at micro sites with abundant lichens, within stands that, overall, have sparse lichen growth (Edmonds and Bloomfield 1984; Kansas and Brown 1996; Stepaniuk 1997).

My results were unclear as to whether caribou were selecting stands with less spruce at the fine scale. Although logistic regression indicated this, a t-test revealed

no statistically significant difference in spruce between used and available stands. There may be a lack of selection for spruce stands at this scale because of the mild snow conditions during all three years of my study. Although caribou may ensure that spruce stands are close by, in case harsh snow conditions arise (as previously discussed), these stands may not have been required during the years of my study.

Seasonal Patterns

Habitats change over the winter, and between winters, as snow conditions fluctuate. Species generally select for a suite of habitats (Helle 1980), but the range of habitats required may not be detected if the temporal scales analysed are too broad. Therefore, it is valuable to divide larger time periods into smaller periods for analyses (Arthur et al. 1996).

At both fine and coarse spatial scales, caribou used habitat differently in early winter compared to late winter, although older stands were generally preferred over younger stands in both periods. Also, caribou used stands over 160 years old to a greater extent in the late winter than in the early winter, similarly to the findings of Bjorge (1984) and Schaefer and Pruitt (1991). This may be related to snow conditions in my study area, which are generally deeper and harder in March, compared to earlier in the winter, for any given year (Edmonds and Bloomfield 1984). The deeper, harder snow may force caribou to increase their consumption of arboreal lichens, which are most abundant in older stands (Chapter 3). Although my study focused on within-year variation in habitat selection, habitat selection patterns

in late winter may be indicative of important habitat during winters with deep or hard snow.

Inter-annual Variation

Caribou habitat use differed among years, which is consistent with past research in this study area (Edmonds and Bloomfield 1984), and elsewhere (Rettie and Messier 2000). In 2000/01, caribou did not prefer older stands to the same extent as in other years. This may be because there were no available data beyond March 15, 2001. According to my seasonal analyses, caribou preferred older stands more during late winter (March 1-31). Since this period was only partially included for 2000/01, my results may be underestimating the importance of older stands for caribou wintering in this area.

Annual analyses also revealed that caribou in 1999/00 used the densest stand category less than during the other two years. This may be attributed to snow conditions. In 1999/00, mean monthly snowfall was 11.2 cm, compared to 41.9 and 24.6 cm in 1998/99 and 2000/01, respectively (November-April data for 1998/99 and 1999/00, November-February data for 2000/01; Grande Cache Airport unpubl. data). Denser stands may be selected for greater snow interception, required less during years with little snow. These findings reinforce the importance of maintaining a suite of habitats for the conservation of a species, since habitat needs may differ substantially from year to year. In general, comparisons of habitat use among years highlights the importance of conducting multi-year studies, to determine average or typical habitat requirements, by looking for dominant patterns (Schooley 1994).

Data Limitations

Currently, forest harvesting is a major industrial activity in the Redrock/Prairie Creek winter range. Of interest to forestry and wildlife managers is the stand age required to meet the habitat needs of caribou. Ideally, research should focus on caribou selection for regenerating cutblocks, to determine the age at which these cutblocks are used by caribou for foraging, or for general habitat use. However, since forest harvesting in this study area has only occurred for about 25 years, the range of cutblock ages required to conduct such an analysis do not exist. Therefore, I analysed stand age selection for all forest stands, most which were initiated by wildfire. Interpretation of my findings must acknowledge that fire and timber harvesting differ in their effects on habitat attributes, such as lichen regeneration (Webb 1998). In fact, if disturbance (e.g., scarification, post-logging erosion) to forest ground cover is minimal, logging may actually retain more lichens than fire, in the short term (Webb 1998), which may decrease the regeneration time for suitable caribou forage. Alternatively, greater retention of organic matter after logging, compared to fire, may enable mosses to invade and crowd out lichens (Racey et al. 1996). Therefore, my results must be applied cautiously to rotation age planning, and adaptive management must be employed.

Habitat use varied throughout the day, which may have influenced my results. This may be due to specific habitat requirements for activities such as bedding, foraging and travelling, which may occur in a regular pattern throughout the day (Maier and White 1998). Analyses using all time periods (rather than the subset used in my analyses) would likely show slightly greater selection for 80-120 year old

stands, and reduced preference for stands 40-80 years, and over 160 years, although the overall trend would not likely differ from my findings. As well, stands with 71-100% canopy closure may be slightly more preferred than my results indicate.

Oberg (2001), using some of the same caribou location data as in my study, found that the assumption of caribou independence may have been violated. She found that, in 1998/99, 1 of 10 potential pairs of caribou were less than 1 km from each other for 25% of the winter. In 1999/00, 7 of 21 potential pairs of caribou were less than 1 km from each other for 26-68% of the winter. I also found a lack of independence between some caribou for 2000/01. However, similarly to Oberg (2001), I chose not to discard data from caribou that spent some time in the same group, primarily because of a limited sample size. Also, none of the caribou spent the entire winter in the same group, which implies that individuals are flexible in their group choice. Presumably, an individual would only remain in a group if their habitat needs are met.

Management Implications

It is typically assumed that habitat selection analyses indicate which habitats are most important for the overall fitness of an animal (Morris 1987; White and Garrott 1990). Ultimately, the important question for wildlife managers is whether the presence, absence, or abundance of certain habitats affects populations. The findings of my research suggest that several habitat characteristics are important to caribou, and a loss of these could affect caribou populations negatively, although demographic analyses were beyond the scope of my research. Since caribou have

been recently designated as threatened, both in Alberta (under the provincial Wildlife Act), and at the national level (COSEWIC 2000), there is an impetus to act conservatively to ensure that caribou have sufficient habitat over the long term.

The results of my study clearly show that older forests are important for caribou at every spatial and temporal scale. There is strong evidence that stands under 80 years old are avoided relative to stands over 80 years, and that stands over 120 years may also be critical for caribou. To maintain these age classes, timber-harvesting rotations must be lengthened beyond what is typical for the forest industry, and older stands must be maintained throughout the caribou range. Although caribou selection for stand age has the most direct implications for activities like timber harvesting, stand density should also be considered for forest management, and denser stands (71-100% canopy closure), should be maintained throughout the winter range.

In west central Alberta, government and industry have been working to define the habitat supply requirements for caribou (Hervieux et al. 1996). The intent is to progress towards managing forest harvesting, and other industrial activities, so that required habitats may be maintained over the long term. Although my study identified the important habitat characteristics for caribou, I did not determine *how much* of the important habitats are required to maintain populations. Others have stressed that sufficient habitat for caribou does not simply mean sufficient habitat for forage requirements (Cumming 1992; Hervieux et al. 1996). Caribou may also require enough good quality habitat to avoid predators, through avoiding alternate prey (Bergerud 1985; Bergerud and Page 1987; Seip 1992; but see Euler et al. 1976

for habitat use in the absence of predators). Also, caribou are thought to avoid predators by existing at low densities, since predators tend to hunt in areas with high densities of prey (Bergerud et al. 1984; Bergerud and Page 1987; Bergerud et al. 1990). If sufficient habitat is not available, caribou may be forced to concentrate in their preferred habitat (Smith et al. 2000), which could lead to higher predation levels (Bergerud and Page 1987), and population declines (Cumming and Beange 1993).

When planning for habitat supply, it will be necessary to take into account not only the forest stand characteristics affected by timber harvesting, but also the implications of other industrial activities (such as oil & gas exploration and development) and natural disturbances (such as fire). These factors may compound the effects of habitat change over time (Dyer et al. 2001; Oberg 2001). The results of my research indicate that caribou select habitats at both 2nd and 3rd orders (Johnson 1980), corresponding to my coarse and fine scales. In related research, I found strong habitat selection for foraging at an even finer scale (Chapter 3). This suggests that habitat supply planning must also occur at multiple scales. Sufficient habitat must be maintained for caribou throughout the entire range, and also within subsets of the range.

My analyses of habitat selection in the early and late winter indicate that caribou may require different habitats depending on snow conditions (also see Chapter 3). Managers must therefore maintain the suite of habitats required by caribou. During late winter, snow is generally deeper and harder than in early winter, which may mimic the snow conditions that prevail during harsh winters. Although harsh winters may only occur occasionally, these winters may limit caribou

populations if sufficient critical habitats are not maintained (Hyvarinen et al. 1977; Reimers 1977; Adamczewski et al. 1986; Nellemann 1996). My analysis of caribou habitat selection in late winter showed that caribou used stands over 120 years old to a greater extent during this period. Therefore, stands over 120 years must be maintained throughout the caribou range to ensure sufficient habitat for harsh winters.

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CHAPTER 3 –MOUNTAIN CARIBOU FORAGING STRATEGIES, RELATIVE TO HABITAT AND SNOW IN ALBERTA

INTRODUCTION

Woodland caribou (*Rangifer tarandus caribou*) populations in Alberta are in decline (Edmonds 1988; Dzus 2001), and their distribution has receded substantially over the past 100 years (Dzus 2001). Consequently, this subspecies was designated as threatened under Alberta's Wildlife Act in 1985 and, after re-evaluation, in 2001. The decline has been attributed, in part, to habitat loss and alteration (Dzus 2001). Therefore, understanding caribou habitat requirements is essential for managing the species. We must understand their requirements under typical conditions and, perhaps more importantly, during harsh or atypical periods. For instance, when snow is deep and/or hard, caribou may alter their foraging behaviour and, in turn, require a unique suite of habitats (Pruitt 1959; Stardom 1975; LaPerriere and Lent 1977; Bloomfield 1979; Darby and Pruitt 1984).

The abundance of forage, in combination with other factors, influences the types of habitats that animals select for feeding (White and Trudell 1980). Caribou forage extensively on lichens, which can be classified into two groups, depending on where they grow. Terrestrial lichens grow in mats on the forest floor, while arboreal lichens grow in trees, suspended from branches. In west central Alberta, caribou generally "crater" (or feed on terrestrial lichens and other forage by digging through the snow) when snow conditions are favourable (Edmonds and Bloomfield 1984; Stepaniuk 1997). Elsewhere, caribou shift to foraging on arboreal lichens when snow is excessively deep and/or hard (Edwards and Ritcey 1960; Bergerud 1974; Rominger

and Oldemeyer 1989). This response, however, is not consistent across all caribou ranges (Vandal and Barrette 1985; Brown and Theberge 1990).

My study focused on forage and habitat selection by one herd of mountain caribou (an ecotype of woodland caribou; Edmonds 1998), in west central Alberta, over variable snow conditions. I predicted that caribou habitat selection relates to forage selection, which in turn relates to snow conditions (Figure 3-1). Since terrestrial and arboreal lichens are abundant in different habitats, I predicted that caribou would select certain habitats for cratering (mainly for terrestrial lichens) and others for feeding on arboreal lichens. Terrestrial lichens are typically abundant in semi-open stands dominated by lodgepole pine (*Pinus contorta*) that are over 75 years old (Edmonds and Bloomfield 1984). By comparison, arboreal lichens, which are very slow growing, thrive in much older stands (Ahti and Hepburn 1967; Stevenson 1986; Rettie et al. 1997). In west central Alberta, arboreal lichens grow best in semi-open subalpine fir (*Abies lasiocarpa*) and white spruce (*Picea glauca*) forests over 130 years old (Edmonds and Bloomfield 1984; Thomas et al. 1996). Thus, I predicted that caribou would switch from cratering in semi-open stands with greater amounts of pine, to feeding on arboreal lichens in old stands with greater amounts of spruce, as snow depth and/or hardness increased.

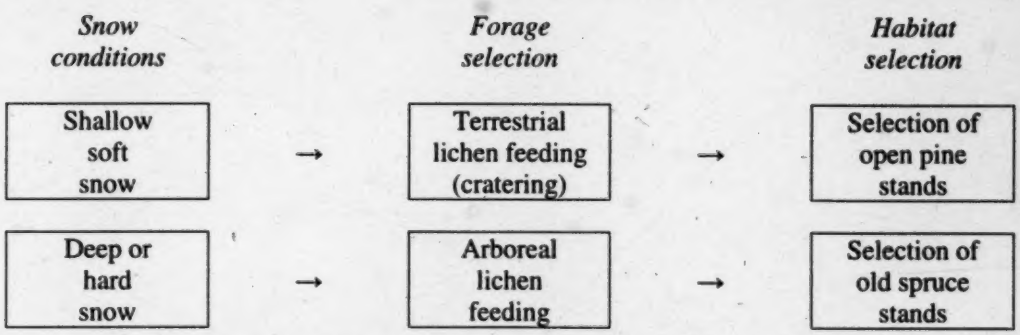


Figure 3-1. Predicted relationship between snow conditions, forage selection and habitat selection of mountain caribou in west central Alberta.

METHODS

Study Area

This study was conducted within the Redrock/Prairie Creek caribou winter range in west central Alberta (54°N, 119°W) (Figure 2-1), which extends north and south of the Kakwa River, along the eastern slopes of the Rocky Mountains. Roughly 300 mountain caribou winter in this area (Brown and Hobson 1998). Annual snowfall at the town of Grande Cache (November-April) ranged from 66.0-295.7 cm (mean = 148.6 cm) from 1974-2000 (Grande Cache Airport unpubl. data).

Tracking Sessions

During the winters of 2000 and 2001, caribou tracks were followed to gather information on habitat use, snow conditions and foraging. Caribou were located primarily through VHF (Very High Frequency) telemetry by Alberta Fish and Wildlife, Grande Prairie. We occasionally followed tracks found opportunistically along snowmobile trails or roads. To increase independence when tracking caribou found this way, we only followed tracks that were spaced at least 10 km apart within

a one week period. In general, groups of caribou were not tracked more than once per week. Tracks that were greater than 3 km from snowmobile access were not followed due to time constraints. The travel path of one caribou was chosen for each tracking session, and was followed for about 2 km.

Foraging and Control Stations

We collected data on habitat, snow conditions and foraging at several "stations" (i.e. plots where detailed data were recorded) along each tracking session (Figure 3-2). We set up stations at the start of the tracking session, at feeding sites (cratering and arboreal lichen feeding), and at controls every 250 m along stretches where there was insufficient foraging to establish a feeding station (see criteria below). Station centres were the middle of cratering or arboreal feeding areas, or at the 250 m point along a travel path, for controls.

Cratering feeding stations were set up when there was more than 3 m^2 of cratering per caribou, over a 20 m stretch of tracking. Individual craters that were not part of cratering stations were recorded separately, and used in calculations of overall cratering activity along the tracking session. Arboreal lichen feeding was recognised by caribou tracks leading up to, and occasionally around, trees; typically fragments of branches and arboreal lichens were lying on the snow beneath. Arboreal feeding differed from cratering in that it was usually spread out along a travel path, and was only loosely clumped in distribution. To accommodate this, we established arboreal feeding stations at the first sign of arboreal feeding, and then added subsequent signs of feeding to this station *as long as the habitat stayed the same*. A change in habitat

was visually estimated, and defined by a change in the maximum or mean tree diameter (by > 5 cm), the percent of spruce (by > 20%) or by an increase/decrease (by > 3) in the number of trees with an arboreal lichen class greater than four (see explanation below). Finally, in the absence of feeding sites along a travel path, control stations were set up every 250 m, starting from the last control station or outer edge of feeding stations.

At each station, we visually estimated overstory stand density (percent of sky covered by the canopy) and the percentage of each tree genus (*Picea spp.*, *Abies spp.*, or *Pinus spp.*) within a 30 m radius around the station centre. Following Armleder (1992), we quantified arboreal lichen abundance on a scale from one to five, by comparing trees in the plot to photographs of trees with varying lichen abundance. We tallied the lichen abundance for all trees within 10 m of the station centre and recorded the number of trees within this same area. In 2001, we also recorded the number of trees in each lichen abundance class, which enabled calculations of total lichen biomass (g), using multipliers outlined by Stevenson et al. (1998).

Snow depth, track penetration and hardness were analysed within 2 m of the station centre. We sampled depth (cm) and track penetration (cm) five times and recorded the mean. Snow hardness was classified once, on a scale from 1 to 4 using a ski pole test (Table 3-1). This method qualitatively tests the vertical hardness of the entire snow pack by forcing a ski pole through the snow, and assessing the difficulty to reach ground.

At cratering stations, we also recorded the area of snow disturbed by cratering, and estimated the number of caribou using the site (by counting parallel sets of tracks

when caribou entered, or left, a feeding site). At arboreal lichen feeding stations, we recorded the number of trees showing evidence of caribou feeding, and again estimated the number of caribou using the area. In 2001, we also quantified the intensity of arboreal lichen feeding, using values similar to Simpson et al. (1985). A value of 1 was recorded for sites where caribou simply approached a tree; 2 described trampling less than half way around a tree; and 3 described trampling more than half way around a tree. For both cratering and arboreal feeding, we recorded feeding activity only for the individual being tracked, whenever possible. Although this could usually be done for arboreal lichen feeding, at cratering sites there were often many animals milling around an area, and feeding of individuals could not be recognised. In these situations, we divided total feeding activity by the estimated number of caribou feeding, to determine feeding per individual.

Statistical Analyses

Foraging Behaviour Over a Range of Snow Conditions

I tested all data for linearity, normality and constant variance prior to analyses, and any deviations from these assumptions are reported in the results. I conducted multiple linear regression to relate cratering and arboreal feeding (per caribou per km) to snow conditions. Measures of snow conditions included maximum depth, maximum hardness, mean depth and median hardness, and were calculated using station data from each tracking session. I analysed arboreal feeding weighted by feeding intensity (i.e. 1, 2 or 3), and without weighting. Since results were the same for both analyses, I only report values using non-weighted data.

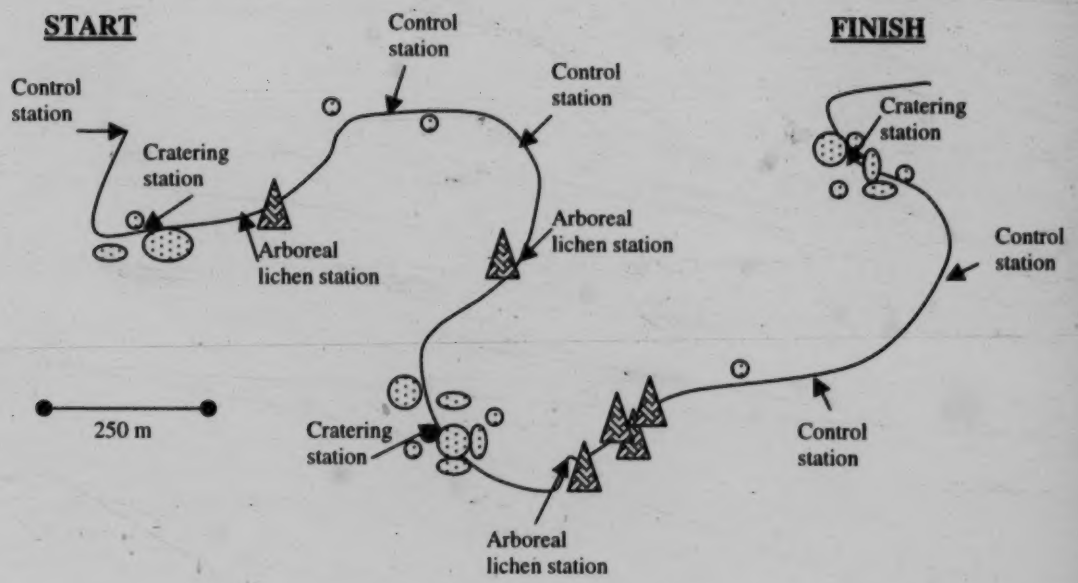


Figure 3-2. Schematic showing a typical winter caribou tracking session in the Redrock/Prairie creek winter range, 2000-2001.

Table 3-1. Descriptions of ski pole test values, used to quantify snow hardness in west central Alberta (2000-2001).

Ski pole test value	Description
1	The snow pack does not have any crust layers, and it is easy to penetrate the ski pole to ground
2	The snow pack has crust layers that are penetrable with minimal force
3	The snow pack has crust layers requiring substantial force to penetrate or the snow pack is hard overall and requires several attempts to penetrate to ground
4	The snow pack is too hard to enable penetration to ground with a ski pole

Selection of Habitat and Snow Conditions for Foraging

Multiple logistic regression (Menard 1995; Alldredge et al. 1998; Boyce and McDonald 1999) was used to analyse selection of habitat and snow conditions at cratering stations and arboreal feeding stations compared to controls (stations without foraging). For all logistic regression analyses, I tested for collinearity using tolerance statistics (threshold of 0.2) and for non-linearity using the Box-Tidwell test (Menard 1995). I also identified residuals using Studentized values, leverage values and dbeta values, following Menard (1995). I pooled all stations, independent of tracking session, and assessed auto-correlation by visually comparing residuals among and within tracking sessions.

To identify the most parsimonious model, I used the drop in deviance test to determine the significance of each independent variable (Menard 1995). This

involves calculating chi-squared test statistics by comparing models with, and without, the variables being tested. I analysed the significance of categorical variables (e.g., hardness) by creating a set of dummy variables. Variables with a $p \leq 0.10$ were retained in the final model. Crater site selection was modelled relative to habitat variables (density and percent of pine in the stand) and to snow variables (depth and hardness). Arboreal feeding site selection was also modelled relative to habitat variables (stand age and percent of spruce) and to snow variables (depth and hardness). To visualise the effect of each significant variable, I plotted univariate logistic function plots. When there was more than one significant independent variable in the final model, I calculated the logistic function for the variable of interest by substituting the mean values for other variables in the equation.

Since stand age was not measured in the field, GPS (Global Positioning System) locations collected at stations were overlaid on Phase 3 forest maps from Weyerhaeuser Company Ltd., to obtain this information. Phase 3 mapping consists of polygons delineated through air photo interpretation, with supplemental information from ground truthing (Alberta Forest Service 1984). I visually checked for location errors and either corrected or removed suspicious locations. Since age data were only available for "productive" stands (greater than 6% crown closure, and cutblocks), analyses involving stand age were restricted to these stands.

Arboreal Lichen Abundance at the Stand Level

I used multiple linear regression to compare stand biomass of arboreal lichens (grams), to stand age and percent spruce. This analysis was restricted to data from

2001, because the number of trees in each lichen class was only recorded in this year, and this information was required for calculating biomass.

RESULTS

We conducted 71 winter tracking sessions: 29 in 2000 and 42 in 2001 (Figure 3-3). Of 598 stations sampled, 131 were cratering sites, 185 were arboreal lichen feeding sites, and 309 were controls. Twenty-seven sites had both cratering and arboreal feeding. For arboreal lichen feeding, only 385 stations were analysed because stand age was not available for inaccurate or missing GPS locations, or for "non-productive" stands. Most of the tracking sessions were north of the Kakwa River due to accessibility, and because a greater number of caribou were relocated here during the tracking periods.

Foraging Behaviour over a Range of Snow Conditions

Three of the 71 tracking sessions were removed from analyses because insufficient data were collected on foraging (there were ≤ 3 stations). Along the 68 tracking sessions analysed, mean cratering activity was 25 m^2/caribou/km (SD = 36.4) and mean arboreal feeding was 4 bouts/caribou/km (SD = 4.73). For all stations, snow depth ranged from 2 to 62 cm (mean = 26.7 cm) and hardness ranged from 1 to 4 (median = 2). Due to two mild winters, the depth of the snow was shallower than average for this area (Grande Cache airport, unpubl. data)

There was no evidence that mean or maximum snow depth, or median or maximum snow hardness, influenced the amount of cratering by caribou ($F = 0.562$,

df = 4, 63, p = 0.691). However, arboreal lichen feeding increased with median snow hardness (F = 12.261, df = 1, 66, p = 0.001, r^2 = 15.7%).

Selection of Habitat for Foraging

On average, cratering sites were denser, and had a higher percent of pine than controls (Table 3-2). Multiple logistic regression revealed that cratering sites were associated with moderately dense stands (around 50% canopy closure), however, there was no relationship with amount of pine (Table 3-3; Figure 3-4). The term **(density)ln(density)** was significant (Box-Tidwell test, chi-squared = 5.246, df = 1, p = 0.022), and was therefore retained in the final model. 70.23% of the stations were correctly classified as cratering sites or controls, and there was no evidence of lack of fit (Hosmer-Lemeshow, chi-squared = 3.471, df = 7, p = 0.838). The odds ratios listed in logistic regression tables (Table 3-3; Table 3-4; Table 3-5; Table 3-6) indicate the percent change in the probability of cratering, or arboreal feeding, associated with a 1% change in the habitat or snow variable.

Sites with arboreal feeding were older, and had greater percentages of spruce than controls (Table 3-2). Both variables contributed to the highly significant difference between arboreal feeding sites and controls (Table 3-4; Figure 3-4). 63.4% of the stations were correctly classified as arboreal feeding sites or controls, and there was no evidence of lack of fit of the model (Hosmer-Lemeshow, chi-squared = 7.761, df = 8, p = 0.457).

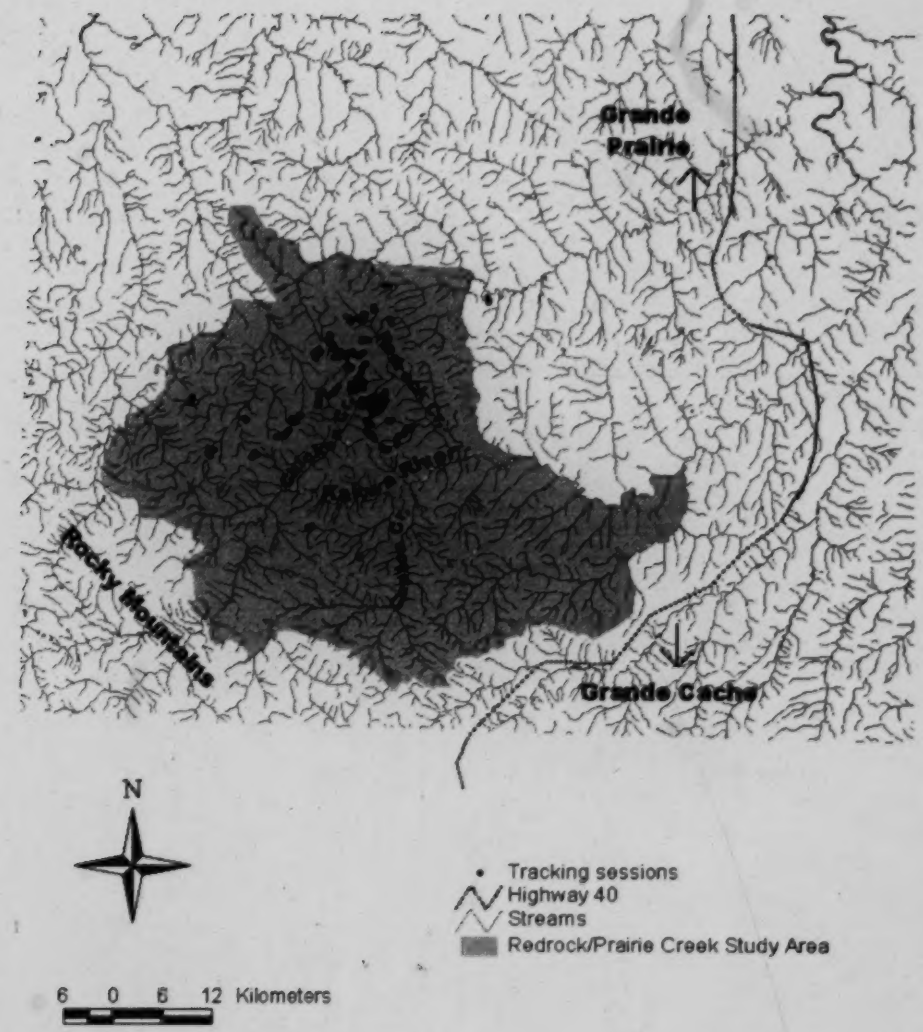


Figure 3-3. Map of Redrock/Prairie Creek study area showing the distribution of snow-tracking sessions over two winters (2000-2001).

Table 3-2. Minimum, maximum and mean (median for snow hardness) values for forest stand and snow variables at foraging sites and controls, in west central Alberta (2000-2001).

Variable	Site	Minimum	Maximum	Mean (Median)
Stand density	Cratering	0%	70%	29.1%
	Control	0%	80%	23.4%
Percent pine	Cratering	0%	100%	57.8%
	Control	0%	100%	48.0%
Stand age	Arboreal	36 years	226 years	155.4 years
	Control	3 years	226 years	132.7 years
Percent spruce	Arboreal	0%	100%	39.3%
	Control	0%	100%	23.0%
Snow depth	Cratering	2 cm	50 cm	23.5 cm
	Arboreal	2 cm	59 cm	27.1 cm
	Control	2 cm	62 cm	27.8 cm
Snow hardness	Cratering	1	3	1
	Arboreal	1	4	2
	Control	1	4	2

Table 3-3. Logistic regression model describing stand characteristics important for selection of cratering sites, by caribou wintering in west central Alberta (2000-2001). P-values for habitat variables were calculated using a drop in deviance test, while the p-value for the constant variable was from a Wald's test.

Crater site selection for stand characteristics (n = 440, model chi-squared = 15.606, df = 2, p < 0.001)				
Variables retained in the model	**B**	**SE**	**p**	**Odds Ratio**
Density	0.155	0.063	0.000	16.81%
(Density)ln(density)	-0.032	0.015	0.022	-3.13%
Constant	-2.024	0.379	0.000	
Variables removed from the model				
Pine	-	-	0.336	-

Table 3-4. Logistic regression model describing the stand characteristics important for selection of arboreal lichen feeding sites, by caribou wintering in west central Alberta (2000-2001). P-values for habitat variables were calculated using a drop in deviance test, while the p-value for the constant variable was from a Wald's test.

Arboreal feeding site selection for stand characteristics (n = 385, model chi-squared = 26.622, df = 2 , p < 0.001)				
Variables retained in the model	**B**	**SE**	**p**	**Odds Ratio**
Age	0.008	0.002	0.004	0.76%
Spruce	0.009	0.004	0.027	0.93%
Constant	-1.753	0.344	0.000	

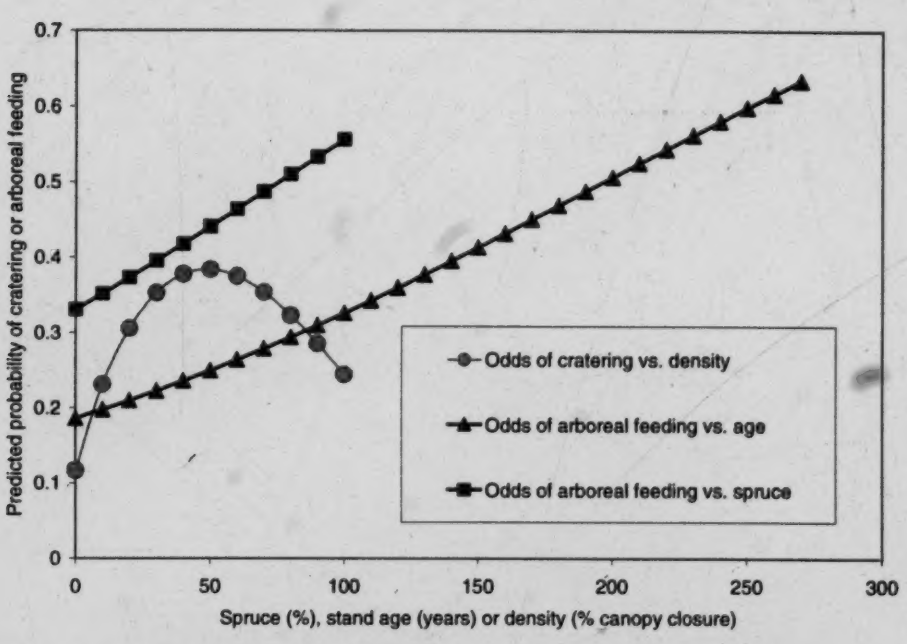


Figure 3-4. Predicted probability of cratering or arboreal lichen feeding relative to stand characteristics, for caribou wintering in west central Alberta (2000-2001).

Selection of Snow Conditions for Foraging

Crater sites had shallower, softer snow than controls (Table 3-2) and multiple logistic regression confirmed that both snow variables were associated with the predicted probability of cratering (Table 3-5; Figure 3-5). 70.23% of the stations were correctly classified as cratering sites or controls and there was no evidence of lack of fit (Hosmer-Lemeshow, chi-squared = 11.805, df = 8, p = 0.160). Three sites had high Studentized values (>2, although <3). I examined these data and although the sites were atypical (cratering with hardness = 3 and depths >30 cm), the values were plausible and not removed from analyses. There was no apparent difference between snow conditions at arboreal sites compared to controls (Table 3-2), and there was no evidence of a relationship between the predicted probability of arboreal lichen feeding and snow conditions (Table 3-6).

Arboreal Lichen Abundance at the Stand Level

The biomass of arboreal lichens (grams) was log transformed, to conform to constant variance and normality assumptions. Multiple linear regression indicated that both the percent of spruce and age were significant predictors of arboreal lichen biomass within 10 m of the station centre ($F = 29.100$, df = 2, 266, $p < 0.001$, $r^2 =$ 18.0%; Table 3-7; Figure 3-6). A 1 year increase in stand age was associated with a multiplicative increase in the median grams of arboreal lichen of 1.004, while a 1% increase in the amount of spruce was associated with a multiplicative increase in the median grams of arboreal lichens of 1.012.

Table 3-5. Logistic regression model describing the snow conditions important for selection of cratering sites, by caribou wintering in west central Alberta (2000-2001). P-values for snow variables were calculated using a drop in deviance test, while the p-value for the constant and categorical variables were from a Wald's test. Large odds ratio values for hardness categories are because of extremely low use of the 4th hardness category.

Crater site selection for snow conditions (n = 440, model chi-squared =28.406, df = 4, p < 0.001)				
Variables retained in the model	**B**	**SE**	**p**	**Odds Ratio**
Depth	-0.028	0.010	0.000	-2.78%
Hardness			0.004	
Hardness (1)	6.153	10.135	0.544	46888.10%
Hardness (2)	6.022	10.134	0.552	41137.79%
Hardness (3)	4.571	10.152	0.653	9566.31%
Constant	-6.113	10.140	0.547	

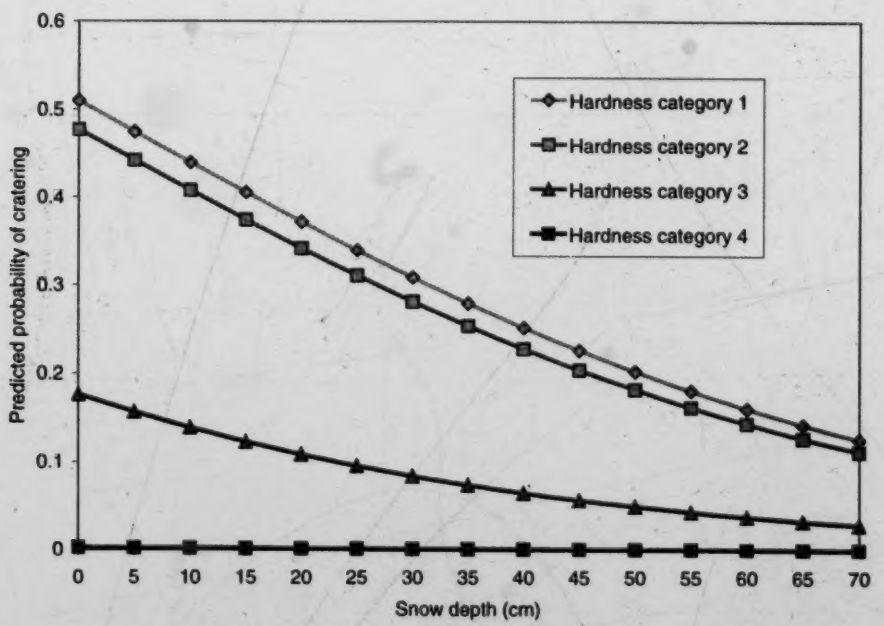


Figure 3-5. Predicted probability of cratering relative to snow depth and hardness, for caribou wintering in west central Alberta (2000-2001).

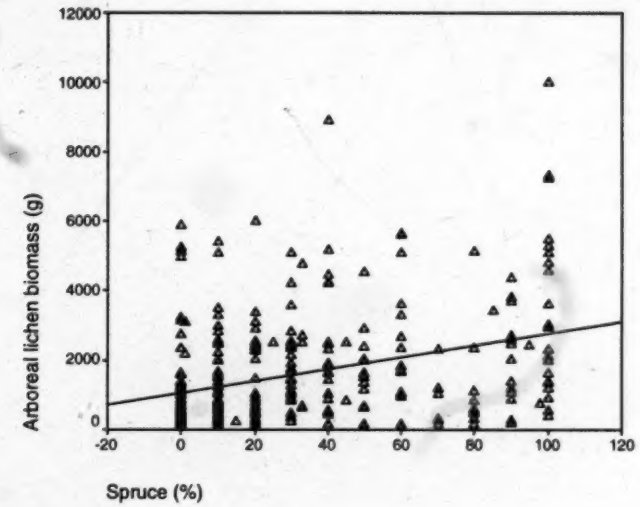
Table 3-6. Logistic regression model relating snow conditions to selection of arboreal feeding sites, by caribou wintering in west central Alberta (2000-2001). P-values were calculated using a drop in deviance test.

Arboreal feeding site selection for snow conditions (n = 494, model chi-squared = 1.548, df = 2, p = 0.4612)				
Variables removed from the model	**B**	**SE**	**p**	**Odds Ratio**
Depth	-	-	0.632	-
Hardness	-	-	0.279	-

Table 3-7. Multiple linear regression model describing the relationship between arboreal lichen biomass within 10 m of station centers, to stand characteristics in west central Alberta (2001).

Arboreal lichen abundance (log) relative to stand characteristics (n = 269, F = 29.100, df = 2, p < 0.001)			
Variables retained in the model	**B**	**SE**	**p**
Age	0.004	0.001	0.001
Spruce	0.012	0.002	0.000
Constant	5.909	0.184	0.000

A



B

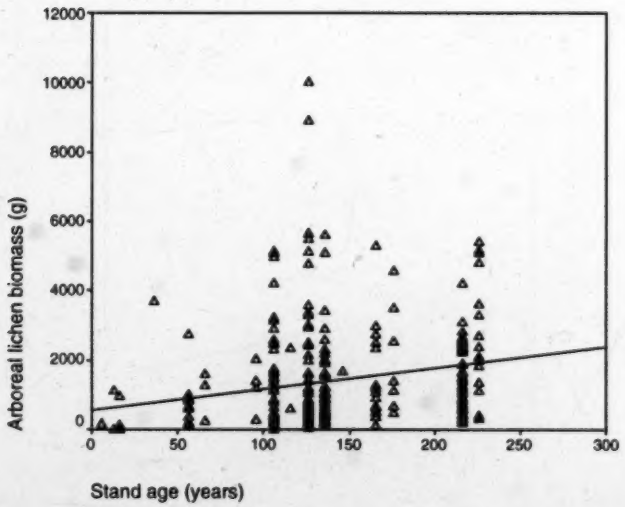


Figure 3-6. Arboreal lichen biomass (grams) within 10 m of the station center, relative to percent spruce (**A**) and stand age (**B**) in west central Alberta (2001).

DISCUSSION

Snow conditions are known to affect the forage and habitat requirements of *Rangifer* around the world (Henshaw 1968; Bergerud 1974; Stardom 1975; Darby and Pruitt 1984). While many researchers in west central Alberta have recognised that snow influences caribou forage and habitat use (Bjorge 1984; Edmonds and Bloomfield 1984; Thomas et al. 1996; Stepaniuk 1997), there has been little research to quantify these effects. In particular, the importance of arboreal lichens during periods of harsh winter snow conditions has not been examined (Stepaniuk 1997; Brown and Hobson 1998).

Foraging Behaviour over a Range of Snow Conditions

I found that caribou did not crater less when snow was deeper and harder, but they did feed on arboreal lichens more when snow was harder. This concurs, in part, with research elsewhere, where caribou feed on terrestrial forage when snow conditions enable cratering, but shift to arboreal feeding when snow becomes deep and/or hard (Bergerud 1974). In areas with very deep snow, caribou feed exclusively on arboreal lichens (Edwards and Ritcey 1960; Simpson et al. 1985; Rominger and Oldemeyer 1989). Although caribou may be physically able to dig through deep, hard snow, the benefits gained from forage may not balance the energetic costs of digging (Fancy and White 1985).

I may not have detected a decline in cratering, as snow depth and hardness increased, because of two relatively mild, low-snow winters in my study area. In other regions, caribou altered their habitat or foraging behaviour in response to snow

depths of 60-70 cm (Pruitt 1959; Henshaw 1968; Bergerud 1974; Stardom 1975; Darby and Pruitt 1984). The mean snow depth in my study area was only 26.7 cm (range = 2-62 cm). Alternatively, I may not have detected a decline in cratering if caribou used stands with less abundant terrestrial forage (e.g., denser stands) as snow depth and hardness increased. To attain the same amount of forage, caribou may have to crater more while using these less productive stands (Thing 1977).

Selection of Habitat for Foraging

Caribou selected moderately dense stands (around 50% canopy closure) for cratering. In the same study area, Edmonds and Bloomfield (1984) found that terrestrial lichens were most abundant in semi-open stands dominated by pine. My findings for density are consistent with the hypothesis that animals feed in habitats with more abundant forage. However, while caribou cratered in stands with a higher mean percent of pine (compared to controls), pine was not significant in the logistic model. Thus, stand density alone may sufficiently predict the probability of cratering.

I found that caribou fed on arboreal lichens in older stands with higher percentages of spruce. These results concur with Thomas et al. (1996), who found that during harsh snow conditions (when caribou were expected to feed on arboreal lichens), caribou in some west central Alberta ranges moved into spruce and fir dominated stands over 130 years old. Edmonds and Bloomfield (1984) also reported that caribou in my study area moved more than 20 km to areas of old forest, when snow was deeper than 60 cm, or when there was crusting of snow layers. Woodland

caribou elsewhere in Canada also move into old forest when snow depths increase (Darby and Pruitt 1984; Schaefer and Pruitt 1992).

The forest stands selected for arboreal feeding are consistent with the distribution of arboreal lichens. Arboreal lichens are more abundant in older stands, and in stands with more spruce, as found by others, and confirmed by my research (Ahti and Hepburn 1967; Bloomfield 1979; Thomas et al. 1996; Rettie et al. 1997; Figure 3-6). In west central Alberta, Edmonds and Bloomfield (1984) found that arboreal lichens were most abundant in forests over 130 years, and in spruce stands, and Thomas et al. (1996) found a greater abundance on widely spaced fir and spruce trees. Research in Saskatchewan found that arboreal lichens were most abundant in black spruce (*Picea mariana*) stands over 90 years (Rettie et al. 1997). Edmonds and Bloomfield (1984) proposed that caribou do not select older spruce stands because of arboreal lichen abundance, but because snow is more shallow and soft, and therefore more favourable for cratering during harsh snow conditions. However, my results suggest that caribou do, in fact, select relatively old spruce stands for arboreal feeding.

Selection of Snow Conditions for Foraging

As discussed previously, caribou altered their foraging strategy in response to snow conditions, with greater overall arboreal feeding when snow was harder. I also analysed cratering and arboreal lichen feeding in relation to site-specific snow conditions. I found that caribou selected shallower, softer snow for cratering at the site level, even though, overall, they did not crater less when snow conditions were

harsher. This finding agrees with others, who found that *Rangifer* select areas of shallow snow for cratering (LaPerriere and Lent 1977; Nellemann 1996; Johnson 2000; but see Stepaniuk 1997). My results suggest that caribou are sensitive to changes in snow depth, even when snow is shallow. This concurs with Henshaw (1968), who found that snow deeper than 15 cm led to a reduction in continuous cratering, and with Bergerud and Nolan (1970), who found that snow deeper than 25 cm reduced a caribou's ability to detect terrestrial forage.

I did not find that arboreal lichen feeding sites were associated with deeper, harder snow, even though, overall, there was an increase in arboreal feeding with snow hardness over the winter. This may be because the old, spruce stands selected for arboreal feeding generally have greater snow interception, which would reduce snow depths (Edmonds and Bloomfield 1984). My findings contrast Johnson (2000), who found that arboreal lichen feeding was associated with deeper, harder snow for caribou in northeastern British Columbia.

Data Limitations

Although significant, relationships between feeding site selection and habitat attributes were somewhat weak. This is likely because forest overstory attributes only partially explain the distribution and abundance of lichens (Kansas and Brown 1996; Thomas et al. 1996), and lichen abundance only partially explains where caribou feed. Variables other than food abundance and snow conditions are thought to influence habitat selection, notably predation (Bergerud 1985; Seip 1992; Bergerud 1996). Also, my predictions for terrestrial foraging are based on the assumption that

caribou are foraging for lichens, but other forage is often consumed (Bergerud 1996; Thomas et al. 1996).

Errors in quantifying arboreal lichen feeding may also have affected my results. In the field, we recognised arboreal feeding by caribou tracks leading to a tree, and by lichen fragments scattered around the base of these trees. However, we could not confirm that caribou fed on arboreal lichens at these sites. More importantly, however, is the unknown number of arboreal feeding sites that were missed. I found a mean of 4 bouts of arboreal feeding/caribou/km, which is much less than the mean of 25 m^2 of cratering, over the same distance. However, more subtle arboreal feeding (such as caribou simply turning their heads to forage on nearby trees, and not approaching trees) was likely missed. Although the methods I used provide a good index of arboreal feeding, my research, and research in the past, may be greatly underestimating the amount of arboreal feeding occurring in west central Alberta.

Stand age data for my habitat selection analyses were taken from Phase 3 forest inventory maps, which were delineated based on air photo interpretation, fire history information and ground truthing. However, it is important to note that this age information focuses on tree age, rather than stand age. Trees within a stand may be much younger than the stand itself, since several successional stages may be required before the establishment of certain tree species. For example, a stand with 150 year old spruce trees typically takes more than 150 years to establish, because spruce often grows up under a canopy of pine (Beckingham et al. 1996). Also, stand age is difficult to interpret from air photos, and may be inaccurate (Rettie et al. 1997).

An important consideration in interpreting the results of all habitat and forage selection studies is the influence of spatial scale (Johnson 1980). Weak or non-existent habitat selection trends may occur if an animal has selected habitats at a broader scale (Johnson 1980; Thomas and Taylor 1990). In this study, I explicitly looked at selection of habitats for foraging compared to controls (i.e., general habitat use sites). However, in Chapter 2, I found that caribou also selected habitats for their home range, and for general habitat use within their home range. In particular, I found that caribou selected older stands at these broader scales, which could reduce the strength of the relationship between stand age and arboreal lichen foraging. Nevertheless, I still found a strong relationship at this finer scale.

Management Implications

My study differs from many caribou habitat selection studies in that I analysed selection for overstory attributes routinely mapped for forest inventory (e.g., species composition, density and age). Results from this type of analyses facilitates long-term land-use planning, since forest inventory mapping is the most detailed vegetation data available for much of Canada (Leckie and Gillis 1995). In contrast, many caribou studies focus on finer scales, such as lichen selection (e.g., Frid and Alexander 1995; Johnson 2000), which are currently less applicable for management. Fine scale information, such as the availability of lichens, is difficult or impractical to map, and is therefore more difficult to use in landscape level management.

My analyses focused on caribou selection for forested stands, in part because of data restrictions, since stand age was only available for forested stands. Although

caribou commonly use non-forested habitats (e.g., meadows) (Bjorge 1984; Edmonds and Bloomfield 1984), forested habitats are more likely to be affected by human activities, such as timber harvesting. Land-use management should focus both on the forested habitats found to be important in my research, as well as non-forested habitats found to be important by past research in west central Alberta.

Stands with around 50% canopy closure were selected for cratering, and older spruce stands were selected for arboreal feeding. Therefore, management for caribou habitat must ensure that sufficient supplies of these habitats are distributed throughout the caribou range. In particular, rotation ages for forest harvesting must take into account the strong preference for older stands.

In addition, I found that snow conditions in west central Alberta affect the habitat requirements of caribou. Although caribou may require specific wintering habitats for only short periods, or for the occasional harsh winter, these habitats may be critical for long-term population survival (Thomas et al. 1996). Since limited forage can negatively affect calf survival (Adamczewski et al. 1988) and population viability (Hyvarinen et al. 1977), range carrying capacity may depend on forage availability during periods of harsh snow conditions (Reimers 1977; Gates et al. 1986; Nellemann 1996; but see Bergerud 1996). This raises difficult management issues, since competition with forestry companies for very old timber stands is increasing within the caribou ranges of west central Alberta (Hervieux et al. 1996).

Maintaining sufficient supplies of habitat may be necessary so that caribou can exist at low densities in their preferred habitats, and avoid predators through avoiding alternate prey (Hervieux et al. 1996). Although small groups of caribou

travel together, these groups may spatially separate from one another to avoid predation, since wolves focus on hunting in areas with high densities of prey (Bergerud et al. 1984; Bergerud and Page 1987; Seip 1992). Also, as snow conditions change over the winter, caribou may require different portions of their range, and they may require alternate habitats locally (Bergerud 1974; Thomas et al. 1996). Therefore, it is critical to maintain sufficient habitat at both local and regional scales.

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CHAPTER 4 - THESIS CONCLUSIONS

I analysed habitat selection by mountain caribou, an ecotype of woodland caribou (*Rangifer tarandus caribou*; Edmonds 1998), at multiple spatial scales, and over a range of snow conditions. I demonstrated that mountain caribou in west central Alberta were highly selective in their habitat choice. My findings were generally consistent with the hypothesis that caribou select habitats to reduce predation risk at coarser scales, while focusing on forage selection at finer scales. However, as previously discussed, these hypotheses are not mutually exclusive. In addition, I found that there were differences in habitat selection among time periods, among seasons, among years, and under different snow conditions. Although there has been past habitat research in west central Alberta, my research further defines the specific habitat needs of these caribou, and is the first attempt to examine multiple scales.

For home range selection within the larger study area, caribou selected stands over 80 years old, with the highest preference for 120-160 year old stands. They also preferred stands with 71-100% crown closure relative to all other stands. At a finer scale, for general habitat use within home ranges, caribou showed the highest preference for stands over 160 years old, and avoided stands less than 120 years (relative to stands over 160 years). They continued to select denser stands (71-100% most preferred), but to a lesser extent, since only stands with less than 30% canopy closure were relatively avoided. At the finest scale analysed, caribou selected moderately dense stands (around 50% canopy closure) for feeding on terrestrial

lichens through cratering (i.e. digging through the snow). At this fine scale, they also selected older stands with a high percent of spruce, for feeding on arboreal (tree) lichens. Caribou selected many of the same habitat attributes at multiple scales, which reinforces their importance (Boyce and McDonald 1999; Rettie and Messier 2000). For example, older stands were selected at all scales, even though older forest was highly available at each level (because it had been selected for at coarser scales).

I also found evidence that snow conditions influenced habitat selection. For home range selection and general habitat use, caribou showed a greater preference for older stands in the late winter, when snow was generally deeper and harder than in the early winter. This is consistent with greater arboreal feeding during harsh snow conditions, since arboreal lichens were found to be more abundant in older stands. In addition, caribou fed on arboreal lichens more when snow was harder, and selected areas of relatively shallow, soft snow for cratering.

MANAGEMENT IMPLICATIONS

In Alberta, the West Central Alberta Caribou Committee (WCACSC), and the Boreal Caribou Committee (BCC) - comprised of government, industry, and university representatives - focus on integrating caribou needs with industrial activity. Both committees were established in response to an Alberta government policy, released in 1991 (Information Letter 91-17), which stipulated that industrial activity can only continue to occur on caribou ranges as long as the integrity and supply of caribou habitat is maintained. The WCACSC focuses on caribou ranges in west central Alberta, which include three migratory mountain ecotype herds (Redrock/Prairie Creek, Narraway and A la Peche), two sedentary mountain ecotype

herds (South Jasper and North Banff), and one sedentary boreal ecotype herd (Little Smoky) (Brown and Hobson 1998).

A major task of the WCACSC is to develop guidelines for industrial activity on caribou ranges. A clear understanding of caribou habitat requirements is necessary for appropriate application of these guidelines. For example, the guidelines state that "adequate current and long term supply of quality caribou habitat within each caribou range will be specifically identified, planned for, and provided", and they require that "caribou habitat supply be considered and provided for during timber management planning" (WCACSC 1996). The guidelines also specify that they will be updated, as required, based on new research information. Since managing habitat for caribou can have substantial costs for industry (Armstrong 1998; Brown 1998), it is necessary to make decisions based on accurate information. The habitat supply subcommittee of the WCACSC has been working towards documenting current habitat and forecasting future habitat, which requires information about typical caribou habitat requirements, as well as their requirements during potential "critical" periods, when snow conditions are harsh.

The results of my research point to several specific management recommendations that should be incorporated into long-term planning for forest harvesting and other industrial activities on caribou ranges. Many recommendations specific to the timber industry have been proposed previously, for west central Alberta and elsewhere (Racey et al. 1991; Cumming and Beange 1993; Hervieux et al. 1996; Armstrong 1998). When planning for the habitat needs of caribou, the suite of required habitats must be considered. In general, habitat must be managed over

large spatial and temporal scales (Armstrong 1998), and the cumulative impacts of all industrial activities must be considered (Edmonds 1998). Managers must also ensure that caribou have sufficient areas of preferred habitat to avoid alternate prey and, consequently, predators (Cumming 1992; Seip 1992; Cumming and Beange 1993). My specific recommendations are:

1. At the broadest scale, for home range selection, ensure sufficient stands over 80 years, with canopy closures greater than 70%, are available throughout each caribou range;
2. At a finer scale, for general habitat use, ensure sufficient stands over 120 years, with canopy closures greater than 30%, are available throughout each caribou range;
3. For terrestrial lichen foraging, ensure moderately dense stands (around 50% canopy closure) are available throughout each caribou range; and
4. For arboreal lichen foraging, ensure sufficient spruce stands over 120 years old are available throughout each caribou range.

Without sufficient habitat, caribou populations are very likely to decline (Thomas 1998). Thus, a system must be formulated to determine *how much* habitat must be maintained for caribou over the long term. This might focus on the spatial needs of caribou, in relation to population density targets (Hervieux et al. 1996), natural disturbance regimes (Seip 1998), or comparisons of caribou population trends, over a range of landscape conditions. For example, a promising approach is currently being implemented in northern Alberta (BCC 2001). Here, habitat targets required for maintaining stable populations are being devised by relating population trends, for

several herds, to the level of industrial development within each range. To be successful, any approach must incorporate the cumulative effects of human activities. Although caribou habitat selection may differ slightly among ranges in west central Alberta, results from my research provide a starting point from which to manage habitat across west central ranges.

Provincial and national endangered species policies, and pending legislation, have heightened the profile of caribou management in Alberta. In 1996, Alberta signed the National Accord for the Protection of Species at Risk (CESCC 1996; hereafter referred to as the Accord), which established a commitment to the recovery of threatened and endangered species. Woodland caribou are covered under this Accord, since the subspecies has been listed as threatened at the national level (COSEWIC 2000), and at the provincial level, under Alberta's Wildlife Act. In 2001, the provincial Endangered Species Conservation Committee (ESCC), and the responsible Minister, reaffirmed the threatened designation of caribou in Alberta. To meet caribou conservation requirements at both provincial and national levels, many aspects of caribou biology must be considered. In particular, habitat has been identified as a key factor under the Accord, the proposed federal Species at Risk Act, and proposed amendments to the Alberta Wildlife Act.

To be successful, the management options outlined above require substantial public support, and strong commitment from the Alberta government. Knowledge provides just the first step in caribou conservation. An essential next step is applying this knowledge to manage the caribou, the landscapes upon which they rely, and the human activities that affect these landscapes. The current industrial guidelines for

west central Alberta (WCACSC 1996), although useful for project specific mitigation, do not provide specific direction on larger issues of habitat supply and cumulative effects assessment. Current initiatives in west central Alberta (through the WCACSC habitat supply subcommittee), and elsewhere in the province (through the BCC's recently ratified strategic plan and guidelines), provide encouraging opportunities to address habitat concerns at a strategic level.

FUTURE RESEARCH

Stand age was an important factor for caribou habitat selection at all spatial and temporal scales. Since stand age is likely to be a major focus of forest management (because timber harvesting affects stand age most directly), it is important to understand the relationship between the true age of a stand, and the age identified on current forest cover maps. The digital forest maps used in my study may not accurately depict stand age, and may, in fact, greatly underestimate it. Stand age is determined from air photos, which focus on tree age. However, a stand may be older than individual trees, because of successional pathways (Beckingham et al. 1996). In west central Alberta, some stands may first be colonised by pine, which is succeeded by spruce. Therefore, the age of spruce trees may not accurately represent the age of the stand, nor the amount of time required for the development of present stand attributes.

As discussed in Chapter 2, my analysis of caribou habitat selection incorporated stand age information mainly from stands initiated by wildfire (not timber harvesting). This was necessary since there has only been harvesting in my study area for about 25 years. However, since the forest may regenerate differently

after harvesting, future research should determine when caribou begin using these harvested stands again, and when they stop avoiding areas adjacent to young forest. Opportunities for this type of research will arise as existing cutblocks age.

Additional research on habitat selection will further assist in planning for caribou habitat supply in west central Alberta. Of great importance to caribou may be the size of habitat patches (Racey et al. 1991; Armstrong 1998), and the spatial arrangement and juxtaposition of habitats (Bjorge 1984; Servheen and Lyon 1989; Stuart-Smith et al. 1997). Knowledge about caribou selection for patch size and distribution would assist managers in designing harvesting layout. There currently exist caribou location data (including that used in my study), and forest cover data, which will enable these types of analyses.

Finally, future research must follow an adaptive management approach, as caribou ranges in Alberta continue to be affected by industrial development. It is necessary to use the best information available today to plan for habitat supply. However, caribou population and habitat supply trends must be carefully monitored, and management approaches must be adapted to reflect new information.

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